STOPOVER ECOLOGY OF SEMIPALMATED SANDPIPERS (*CALIDRIS PUSILLA*) AT COASTAL DELTAS OF THE BEAUFORT SEA, ALASKA

By

Roy T. Churchwell

RECOMMENDED:

Dr. Tuula Hollmen

Dr. Kris Hundertmark

Dr. Arny Blanchard

Dr. Kenneth Dunton

Dr. Rudiger Gens

Dr. Abby Powell
Advisory Committee Chair

Dr. Kris Hundertmark
Chair, Wildlife Program
Department of Biology and Wildlife

APPROVED:

Dr. Paul Layer
Dean, College of Natural Science and Mathematics

Dr. John Eichelberger
Dean of the Graduate School

8 December 2015
Date

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A

DISSERTATION

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

Roy T. Churchwell, M.S.

Fairbanks, AK

December 2015

Abstract

Avian migration is one of the wonders of the natural world. Stored fats are the main source of nutrients and fuel for avian migration and it is assumed the fat deposition at stopover sites is a critical component of a successful migration. Stopover sites are crucial in the successful migration of many birds, but particularly for arctic-breeding shorebirds that migrate long distances from breeding to wintering grounds. Despite the importance of stopover sites, it is often difficult to determine the importance of these sites to migrating shorebirds.

I investigated three aspects of stopover ecology of Semipalmated Sandpipers (*Calidris pusilla*) foraging at coastal deltas on the Beaufort Sea coast, Alaska. First, I quantified the spatial and temporal distribution and abundance of the benthic macroinvertebrate community living within the mudflats. I found that there were two ecological groups of macroinvertebrates using river deltas, one originated in terrestrial freshwater habitats and most importantly could withstand freezing in delta sediments over the winter, and the other originated from the marine environment, could not withstand freezing and had to migrate to intertidal habitats each summer from deeper water areas that did not freeze over the winter. Stable isotope analysis allowed me to describe the origin of carbon consumed by invertebrates in intertidal habitats. I predicted freshwater invertebrates would consume terrestrial carbon, and marine invertebrates would consume marine carbon, but I found that both groups utilized the same carbon, which was a mixture of terrestrial and marine sources. My second research question determined the importance of delta foraging habitat for fall migrating Semipalmated Sandpipers. I mapped the temporal distribution and abundance of birds and quantified this relationship to invertebrate distribution and abundance. I researched fattening rates of shorebirds by measuring triglycerides in the blood of shorebirds I captured. I hypothesized that triglyceride levels would be correlated

with invertebrate abundance and related to habitat quality; however, I found no relationship. Next, I determined shorebird dependence on marine invertebrates using the stable isotope signature of invertebrates and shorebird plasma. I found that shorebird abundance was associated with invertebrate abundance, and that shorebirds did feed almost exclusively on invertebrates from the mudflats later in the season. I did not find a significant difference in habitat quality among the deltas, although more birds were counted at the Jago Delta than at the other two deltas. Finally, I researched the question of how change in water levels due to lunar tides and storm surge events impacted the availability of foraging habitat. I assessed the phenology of Semipalmated Sandpiper migration and how this related to the availability of forage based on abundance, distribution, and accessibility of macroinvertebrates. There was a significant decline in the calories available for forage when there was a lunar tide and when there was a storm surge event. The most foraging habitat was available late in the migration period, while the peak in Semipalmated Sandpiper migration was early in the period. Late in the season there is also a greater chance of a storm surge event occurring due to the lack of sea ice during that period. In summary, I found Beaufort Sea deltas were more diverse than I expected both in macroinvertebrate community and in how shorebirds use the available foraging habitat. After completing this research I feel this habitat is critical to Semipalmated Sandpiper migration; however, there is a real risk of extensive change to these deltas due to future warming with negative consequences for shorebirds.

Table of Contents

List of Figures

Page

List of Tables

Page

List of Appendices

Page

Preface

This dissertation has three main chapters formatted for journal submission. Chapter 2 is published in *Estuaries and Coasts*. Chapter 3 is formatted for publication in *Condor*, and Chapter 4 is formatted for *Waterbirds*. Each of these chapters has several co-authors, many of whom are on my graduate committee. Common names of avian species are either capitalized for bird journals (Chapters 1, 3, 4, and 5) or not for ecological journals (Chapter 2).

My research would not have been possible without the financial and logistical support of many people and agencies. The National Fish and Wildlife Foundation, Bureau of Ocean Energy Management, US Fish & Wildlife Service Arctic National Wildlife Refuge, and the Arctic Landscape Conservation Cooperative funded this study. I had logistical support from the Arctic National Wildlife Refuge, USGS Alaska Cooperative Fish and Wildlife Research Unit, Institute of Arctic Biology, and Manomet Conservation Sciences. I had lab support from the Mark Wipfli aquatic invertebrate lab, Alaska Stable Isotope Facility, University of Alaska Forestry Soil Sciences Lab, the Alaska Monitoring and Assessment Program, and the Alaska Sealife Center.

I would like to sincerely thank all of the field and lab technicians who dedicated many hours to collect and sort through samples. Many have become dear friends, and are now successful scientists in their own right. I am also thankful to the Kaktovik Inupiat Corporation for letting me conduct research on their lands and the people of the village of Kaktovik for their help and friendship.

I would like to thank my committee, especially my advisor, Abby Powell, who showed immense patience in helping me write, and for her guidance along the way. I would also like to thank the rest of my committee: Ken Dunton for insights into estuarine ecology, Arny Blanchard for help understanding benthic macroinvertebrates and statistics, Tuula Hollmen for help with

triglycerides and blood metabolites, Rudi Gens for insights in better uses of GIS, Perry Barboza for his help understanding diet, and Kris Hundertmark for his willingness to help at a moment's notice. Two others, Steve Kendall and Stephen Brown, have helped with this project from its inception with all aspects from development and data collection to editing manuscripts. This research was not possible without you.

Finally, last but not least, I would like to thank several folks who have taught me a great deal in the past. My parents Mary Jo and Stew Churchwell for homeschooling me and giving me an appreciation for education. Dave Reeder taught me how to be a biologist. Pat Heglund, Aaron Holmes, and Steve Herman taught me how to be an ornithologist. Craig Davis, Tim O'Connell, and Sam Fuhlendorf taught me to be a Master. The Malones and Rippees taught me what a home is. Thank you, I am indebted.

1 Introduction

Avian migration is one of the greatest feats of the natural world (Newton 2008). Some species such as the Bar-tailed Godwit (*Limosa lapponica*) can fly for ten or more days traveling thousands of kilometers non-stop (Gill et al. 2005). Just the fact that birds are able to navigate across the world using their own senses is quite incredible (Newton 2008). In order to carry out this natural wonder birds require fuel in the form of fat, which they gain prior to departure or at migration stopover sites. Fat has the highest energy per unit wet mass compared to other tissues (McWilliams et al. 2004, Hua et al. 2013), and some bird species double their weight when preparing for multiday flights (Maillet and Weber 2006).

Birds spend anywhere from one day to several weeks at stopover sites, where they forage on invertebrates to accumulate fat before moving on to the next stop on their migration (Warnock 2010). Short duration stops of a day or two with short distances traveled of hundreds of miles between stops are called a "hop" migration. A "skip" migration has intermediate stopover duration and travel distances between a "hop" and a "jump," when birds spend weeks at a stopover location and travel for thousands of miles to the next stop (Piersma 1987, Warnock 2010). Sites where hundreds of thousands of birds stop each year for weeks at a time are called staging areas, while those sites where birds stop for shorter periods are more generally referred to as stopover sites. Some staging areas have been impacted by human activities, and their importance to shorebirds at the population level has become more obvious as shorebird populations have declined as a result of habitat loss and degradation. The harvest of horseshoe crabs in Delaware Bay (Baker et al. 2004), and reclamation projects on the Yellow Sea (Rogers et al. 2010) are examples of human impacts that have negatively impacted shorebird populations.

Population declines due to impacts at stopover sites where migrant shorebirds normally spend less time have been more difficult to document.

My research on shorebird stopover ecology was spawned from several years of research on the Arctic Coastal Plain and adjoining Beaufort Sea coast. There are ~ 230,000 shorebirds nesting on the eastern Arctic Coastal Plain within the Arctic National Wildlife Refuge (Brown et al. 2007). Many of the species nesting on the coastal plain use the northern coast of the Beaufort Sea as the beginning of the route starting their fall migration (Taylor et al. 2010), and these migrants use river delta mudflats as stopover sites along the way (Taylor et al. 2011, Brown et al. 2012). There are 18 documented species nesting on the coastal plain (Brown et al. 2007), but in migration counts along the coast, 83% of detections were Semipalmated Sandpipers (*Calidris pusilla*) (Brown et al. 2012). Because it is the dominant migrant, the Semipalmated Sandpiper became the focus of my research.

In order to better understand the dynamics of shorebird (Semipalmated Sandpiper) use of delta mudflats along the Beaufort Sea coast, I developed a conceptual model describing the fall migration of shorebirds using these areas as stopover sites (Fig. 1.1). The energy assimilated by the migrant population is influenced by the number of birds available to migrate, which is dependent on the current year's survival and nesting success. Energy assimilated for stored fat at these stopover sites can be influenced by several factors, including time spent at each site, feeding rates, competition with other birds, amount of available habitat, presence of predators, and the distribution and abundance of invertebrate prey. In addition, availability of habitat is impacted by the amount of mudflat exposed depending on water levels. There are further regulations on amounts of available mudflat due to changes in water levels that include changes from lunar tides, freshwater inputs, and storm surges that are determined by the wind speed and

direction. Factors influencing the macroinvertebrate community include lower trophic level meiofauna and bacteria communities, sediment moisture and grain size, carbon and nitrogen nutrients, and salinity.

In order to better understand the complex factors influencing fat assimilation at stopover sites, I focused my research on two broad topics: habitat availability and invertebrate availability and quality. First, I described the ecology of macroinvertebrates found at study area mudflats; this information was lacking and little was known about the benthic community that ultimately supports migrating shorebirds. Second, I investigated shorebird response to the distribution and abundance of macroinvertebrates at delta mudflats, while also considering some of the other factors affecting feeding habitat use such as the presence of predators. Finally, I observed tidal fluctuations were minimal compared to lower latitude coastal areas; however, changes in water level due to storm surge events could be dramatically high. I concluded my research by describing these changes in water level and their impact on the availability of foraging habitat. All of these topics are put into the perspective of stopover ecology of Semipalmated Sandpipers on their first "hops" of fall migration.

1.1 Macroinvertebrate Ecology

The Beaufort Sea is locked in ice for nine months of the year, and although deeper water in lagoons and the ocean do not freeze, the intertidal is frozen solid for most of this period. My first objective was to describe the macroinvertebrate community as well as the distribution and abundance of each taxon because there was no published research describing the intertidal macroinvertebrate community of Beaufort Sea deltas. There are several rivers that drain the northern Brooks Range and Arctic Coastal Plain that terminate at the Beaufort Sea, forming extensive lagoons. I hypothesized the marine and freshwater invertebrates present in river delta

mudflats may use different carbon sources because I expected their feeding ecology to reflect the habitat from which they originated; I analyzed δ13C and δ15N isotopic values for both groups to test this hypothesis. Then, for the most common species of invertebrates, I modeled occurrence and environmental variables (sediment moisture, grain size, carbon, and nitrogen) to determine habitat characteristics that influenced the distribution of these taxa. Furthermore, I described the natural history characteristics of some taxa based on temporal changes in distribution on the delta. Finally, I used the isotopic information for δ15N to chronicle the trophic structure of the invertebrate community.

1.2 Shorebird Feeding Ecology

The first "hop" for Semipalmated Sandpipers on their fall migration is river delta habitat along the Beaufort Sea coast. I investigated shorebird use of three main deltas (Canning, Okpilak/Hulahula, and Jago) on the coast of the Arctic National Wildlife Refuge to determine their significance to migrant shorebirds in terms of stopover habitat. I counted Semipalmated Sandpipers on each delta every three days during fall migration to quantify spatial and temporal use of these sites. I used shorebird distribution data to determine whether their abundance was positively related to invertebrate abundance, which I tested using spatially explicit models. In order to quantify fattening rates, I also captured shorebirds throughout the migration period and collected blood samples. I measured triglyceride levels in the blood as an indicator of fattening rates of shorebirds feeding at these sites. I hypothesized that fattening rate would be positively correlated with invertebrate abundance and that triglyceride levels would be related to habitat quality at each of the deltas. In addition, I used blood plasma from these samples to describe the diet of the birds using δ13C and δ15N isotope analyses. I expected diet analysis to quantify invertebrate taxa consumed by Semipalmated Sandpipers using river delta habitats and to

indicate whether shorebirds were feeding on marine or terrestrial invertebrates. Exclusive use of marine invertebrates would indicate dependence on coastal mudflats, rather than tundra and freshwater habitats for preparation for fall migration.

1.3 Foraging Habitat Availability

The availability of foraging habitat impacts the calories that a shorebird can consume and the number of shorebirds that a given delta can support. Because the daily fluctuation in water levels due to tides is low along the Beaufort Sea, feeding habitat is continuously available under normal conditions. This is unlike coastal areas at lower latitudes, where diurnal tides cover feeding areas periodically creating a strong temporal pattern of shorebird use. Despite a relatively constant availability of foraging habitat along the Beaufort Sea, random storm events can cause surges due to wind-driven changes in water levels that can completely inundate the deltas. I quantified the habitat available to feeding shorebirds in the Beaufort Sea deltas during early, middle, and late migration. Then, I modeled the influence of lunar tides and average surge tides observed during the study on foraging habitat availability during each time period.

In summary, migrant Semipalmated Sandpipers use river deltas on the Beaufort Sea coast as the first stop on their fall migration. Herein I quantify the importance of these deltas as stopover sites on the first "hops" of fall migration. This period is one part of the whole annual cycle of Semipalmated Sandpipers. However, carryover effects from one part of the annual cycle can have significant impacts on later events; sandpipers unable to put on sufficient fat stores may not complete a successful migration to the wintering grounds and thus may not survive until the next breeding season.

1.4 References

Baker, A. J., P. M. González, T. Piersma, L. J. Niles, I. L. S. Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in Red Knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proceeding of the Royal Society of London 271:875–882. doi: 10.1098/rspb.2003.2663.

Brown, S., J. R. Bart, R. B. Lanctot, J. A. Johnson, S. Kendall, D. Payer, and J. Johnson. 2007. Shorebird abundance and distribution on the coastal plain of the Arctic National Wildlife Refuge. Condor 109:1–14.

Brown, S., S. Kendall, R. Churchwell, A. Taylor, and A.-M. Benson. 2012. Relative shorebird densities at coastal sites in the Arctic National Wildlife Refuge. Waterbirds 35:546–554.

Gill, R. E., T. Piersma, G. Hufford, R. Servranckx, and A. Riegen. 2005. Crossing the ultimate ecological barrier: evidence for an 11 000-km-long nonstop flight from Alaska to New Zealand and eastern Australia by bar-tailed godwits. Condor 107:1–20.

Hua, N., T. Piersma, and Z. Ma. 2013. Three-phase fuel deposition in a long-distance migrant, the Red Knot (*Calidris canutus piersmai*), before the flight to high arctic breeding grounds. PLoS ONE 8:1–6. doi: 10.1371/journal.pone.0062551.

Maillet, D., and J. M. Weber. 2006. Performance-enhancing role of dietary fatty acids in a long-distance migrant shorebird: the Semipalmated Sandpiper. Journal of Experimental Biology 209:2686–95. doi: 10.1242/jeb.02299.

McWilliams, S. R., C. Guglielmo, B. Pierce, and M. Klaassen. 2004. Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. Journal of Avian Biology 35:377–393.

Newton, I. 2008. The Migration Ecology of Birds. Elsevier LTD, London.

Piersma, T. 1987. Hop, skip, or jump? Constraints on migration of arctic waders by feeding, fattening, and flight speed. Limosa 60:184–185.

Rogers, D. I., H. Y. Yang, C. J. Hassell, A. N. Boyle, K. G. Rogers, B. Chen, Z. W. Zhang, and T. Piersma. 2010. Red Knots (*Calidris canutus piersmai* and *C. c. rogersi*) depend on a small threatened staging area in Bohai Bay, China. Emu 110:307–315. doi: 10.1071/MU10024.

Taylor, A. R., R. B. Lanctot, A. N. Powell, S. J. Kendall, and D. A. Nigro. 2011. Residence time and movements of postbreeding shorebirds on the northern coast of Alaska. Condor 113:779–794. doi: 10.1525/cond.2011.100083.

Taylor, A. R., A. N. Powell, D. A. Nigro, and S. J. Kendall. 2010. Distribution and community characteristics of staging shorebirds on the northern coast of Alaska. Arctic 63:451–467.

Warnock, N. 2010. Stopping vs. staging: the difference between a hop and a jump. Journal of Avian Biology 41:621–626. doi: 10.1111/j.1600-048X.2010.05155.x.

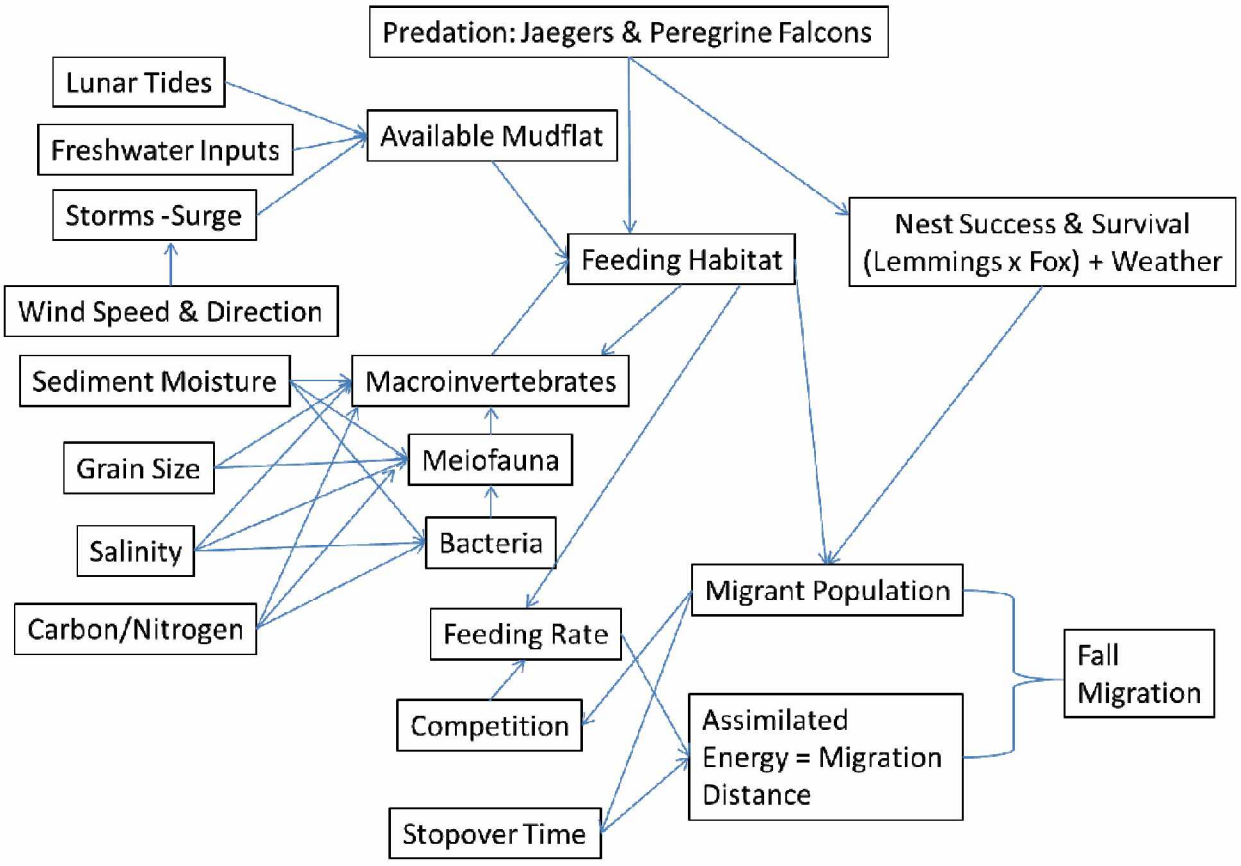

Figure 1.1 Conceptual model describing shorebird stopover ecology at delta mudflats on the coast of the Beaufort Sea, AK.

2 Natural Disturbance Shapes Benthic Intertidal Macroinvertebrate Communities of High Latitude River Deltas[1]

2.1 Abstract

Unlike lower latitude coastlines, the estuarine nearshore zones of the Alaskan Beaufort Sea are ice-bound and frozen up to nine months annually. This annual freezing event represents a dramatic physical disturbance to fauna living within intertidal sediments. Yet, despite the continuous year-to-year episodes of annual freezing, we found evidence that these estuarine deltas are populated by a diverse range of invertebrates that represents both marine and freshwater assemblages. Freshwater organisms like Diptera and Oligochaeta not only survive this extreme event, but a marine invasion of infaunal organisms such as Amphipoda and Polychaeta rapidly recolonizes the delta mudflats following ice ablation. These delta sediments of sand, silt, and clay are fine in structure compared to other Beaufort Sea coastal intertidal sediments. The relatively depauperate invertebrate community that ultimately develops is composed of marine and freshwater benthic invertebrates and is more similar to high arctic invertebrate communities than more boreal estuarine regions in Alaska. The composition of the infauna also reflect two strategies that make life on Beaufort Sea deltas possible, which include a migration of marine organisms from deeper lagoons to the intertidal and freshwater biota that survive the nine-month ice-covered period in frozen sediments. Stable isotopic analyses reveal that both infaunal assemblages assimilate marine and terrestrial sources of organic carbon. These results provide some of the first quantitative information on the infaunal food resources of shallow arctic estuarine systems and the long-term persistence of these invertebrate assemblages.

[1] Published: Churchwell, R.T.C., S.J. Kendall, A.L. Blanchard, K.H. Dunton, A.N. Powell. 2015. Natural disturbance shapes benthic intertidal macroinvertebrate communities of high latitude river deltas. Estuaries and Coasts. *Online at this time*. http://link.springer.com/10.1007/s12237-015-0028-2

Our data help explain the presence of large numbers of shorebirds in these habitats during the brief summer open-water period and their trophic importance to migrating waterfowl and nearshore populations of estuarine fishes that are the basis of subsistence lifestyles by Native inhabitants of the Beaufort Sea coast.

2.2 Introduction

Intertidal habitats are one of the harshest environments (Ellis and Wilce 1961, Gutt 2001) within the Arctic Basin, in which the shoreline is frozen in bottom-fast ice for up to 8-9 months annually. Bottom-fast ice (or the icefoot; Gutt 2001) defines the littoral habitat where water freezes to the sediment and both the water and sediment are encapsulated in ice (Newbury 1983). Ice thickness on the lagoons reaches a maximum of 2 m by spring (Crane 1974), but the freeze depth of intertidal sediments is unknown, although the summer active layer likely freezes completely down to permafrost (Walker 1998). The Beaufort Sea coast is icebound from late October to early July (Newbury 1983) leaving a short open-water window for life to flourish. In summer, the intertidal habitat is important to fish (Craig 1984, Craig et al. 1984) and migrating shorebirds (Taylor et al. 2010) and waterfowl (Moitoret 1983).

We conducted research on the feeding ecology of migrating shorebirds feeding at high latitude river deltas on Alaska's Beaufort Sea coast. These regions are poorly studied and there is a paucity of information on the macroinvertebrate community inhabiting these intertidal habitats. The first documented samples were collected during beachcombing surveys between 1948-1950 (MacGinitie 1959). Between 1950 and 2009 only four studies sampled intertidal habitats in the Beaufort Sea (Crane 1974, Feder and Schamel 1976, Connors and Risebrough 1977, Andres 1989), and none of them used a comprehensive study design to explore this habitat.

At least 19 species of shorebird numbering in the tens of thousands use delta mudflats during the postbreeding period to prepare for and begin their fall migration (Taylor et al. 2010, Brown et al. 2012). Other waterbirds including ducks and geese use the habitat during a premigratory wing molt when they are flightless and vulnerable (Moitoret 1983). Fish including arctic flounder (*Liopsetta glacialis*), four-horned sculpin (*Myoxocephalus quadricornis*), and several anadromous species frequent intertidal waters (Craig 1984). Both waterbirds and anadromous fish are critical subsistence foods for Native inhabitants of the coastal region (Kruse 1991).

Intertidal habitat on the Beaufort Sea coast has been reported as uninhabited by benthic macroinvertebrates (Crane 1974, Feder and Schamel 1976, Gutt 2001), which has been attributed to ice scouring (Ellis and Wilce 1961, Crane 1974). However, at high latitudes scouring is less common in depths < 2 m (Hill et al. 2001), which could be attributed to freeze depths of ~ 2 m (Crane 1974) and the lack of tidal fluctuation. These conditions create a solid ice environment in the intertidal. This ice may provide protection from scouring in shallow-water areas where contrary to the published record reviewed by Gutt (2001), a few unpublished reports have described an intertidal macroinvertebrate community (Connors and Risebrough 1977, Andres 1989). The discrepancy in invertebrate inhabitance in the literature could be the result of the method of invertebrate sampling and research that focused on marine versus terrestrial systems.

River deltas represent the confluence of marine and terrestrial in intertidal habitats that are characterized by widely fluctuating gradients in both physical and chemical parameters (Ellis and Wilce 1961, Anderson 1983, Hill et al. 2001). The conditions create an environment of extremes for benthic inhabitants, especially with respect to temperature and salinity. Typically, physical and environmental gradients structure species distributions, but disturbance is also

known to create species patches (Levin and Paine 1974, Wiens 2000). Annual freezing of sediments is a dramatic disturbance that was thought to halt biological function within intertidal sediments (Anderson 1983), although more recent research revealed that minimal biological function continues in frozen terrestrial soils (Mikan et al. 2002).

Other disturbances augmented by freezing in arctic deltas include drying, elevated salinity, lack of oxygen, and changes in sediment structure (Anderson 1983, Newbury 1983, Gutt 2001). According to the intermediate disturbance hypothesis, moderate levels of disturbance increases diversity (Huston 1979). Implied in the hypothesis is that a highly disturbed environment is defined by a depauperate community when the spatial and/or temporal scale of disturbance modifies the habitat to exclude some species (Huston 1979, Gutt 2001). In highly disturbed areas theory suggests that patch size and distribution of invertebrates may be more limited compared to moderately disturbed areas (Levin and Paine 1974, Wiens 2000). These processes shape intertidal communities, but in the Arctic there has been no research to describe the mechanics of these disturbances or how they might influence marine and terrestrial macroinvertebrates that occupy this habitat.

Because so little is known about the macroinvertebrate communities of arctic intertidal habitats, our primary objectives were to describe and compare the communities at three river deltas on the Beaufort Sea, Alaska. Our first objective was simply to identify the taxa found at each site over two summers (2010 and 2011). We expected species diversity at our sites to be lower compared to temperate regions due to high levels of disturbance from annual freezing. Second, we examined within-year variability of invertebrate abundance during three summer open-water time periods, which we expected to increase as the season progressed, and which also corresponded with shorebird migration. Because invertebrate abundance for a taxon is partially

determined by the environmental factors associated with that habitat patch, we modeled the association between abundance and environmental variables while accounting for spatial and temporal effects. We hypothesized that invertebrate abundance would increase with the proportion of fine sediment and moisture. Environmental variables like grain size and moisture covary with abundance (Yates et al. 1993, Kraan et al. 2010), and we wanted to know if invertebrates are associated with environmental characteristics such as sediment grain size that might be impacted by future climate change or development. Mountain glaciers are a major source of fine sediments, but these glaciers are expected to disappear in the future (Nolan et al. 2011). Third, we mapped the distribution of the common taxa; changes in within-season distribution allowed us to infer natural history characteristics of some taxa.

Finally, we used stable isotope analyses to determine a) the proportion of freshwater and marine carbon in consumer diets, and b) trophic structure. Stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes quantify trophic level and forage dynamics, respectively. Nitrogen isotope values increase about 3.4‰ through fractionation with each step up in trophic level, and thus can estimate relative placement of taxa within a food web (Fry 2006, Dunton et al. 2012). Carbon isotopic values distinguish marine from terrestrial sources based on photosynthetic processes and carbon assimilation through the food chain (Fry 2006). Along the Beaufort Sea coast there is a significant east-west gradient in carbon isotopic values of sediments from the Mackenzie River westward, owing to the large input of terrestrial organic carbon from the Mackenzie and the advection of marine carbon from the Chukchi Sea on the west (Dunton et al. 2006). Within lagoons isotopic signatures of amphipods become more terrestrial with proximity to freshwater inputs and drainages (Craig et al. 1984). We hypothesized that freshwater invertebrate taxa from the delta would have a terrestrial isotopic signature while marine taxa would have a marine

signature, and that there may be a gradient from marine to terrestrial from the lagoon to the high water mark on the delta.

Our studies provide insight into an unexplored invertebrate community and upper trophic levels, and provide a useful baseline for future monitoring and management of these important habitats.

2.3 Methods

2.3.1 Study Area

We conducted our research on the coast of the Arctic National Wildlife Refuge at three high latitude (~70°N) river deltas, the Jago, Okpilak/Hulahula, and Canning, in July and August 2009, 2010, and 2011 (Fig. 2.1). River deltas along the Beaufort Sea are part of a complex lagoon ecosystem. Lagoons vary greatly in size, are usually less than 100 km^2, and are predominant features of the coast. All are estuarine in character, although the magnitude of freshwater inputs can range greatly depending on the presence of rivers or creeks and their associated drainage area (Dunton et al. 2012). Lagoons and river deltas are protected from marine influences by low barrier islands fringing the coast; exchange between the lagoon and marine environment occurs through channels between the islands that are a few meters deep and typically 10 – 40 m wide. During the summer months, these lagoons and their associated littoral zones are warmer and less saline than the adjacent marine environment (Fig. 2.2; Dunton et al. 2012).

Lunar tides on the coast range from -6 cm to 24 cm and average 10.5 cm (NOAA 2010). The lunar tide height only contributes partially to water levels because of a substantial surge effect (Norton and Weller 1984), which is the product of an interaction with the Beaufort Gyre that flows from east to west along Alaska's north coast (Norton and Weller 1984) and

atmospheric pressure, wind speed, and wind direction (Martin 1983, Marsh and Schmidty 1993). The surge makes water level unpredictable because it is derived from weather patterns; however, water level is also relatively constant because the lunar influence is minimal and weather patterns don't often change from day to day.

The weather is relatively warm during July and August (mean 5.7-7.2°C; NOAA 2014), but during the other 10 months the deltas are partially or completely frozen. In September the lagoons start to freeze and ice is well formed by the end of October (Craig et al. 1984). Ice on the lagoons is up to 2 m thick (Craig et al. 1984), and the freezing depth on the mudflat is thought to be substantial because the rivers are completely frozen and the lagoons are nearly so. However, the freeze depth on the deltas has not been measured. Spring breakup normally occurs in June, when rivers flow again and a ring of water forms along lagoon edges. Ice formation and breakup on the deltas are forms of disturbance that occur yearly and may significantly impact the benthic community (Craig et al. 1984, Weslawski and Szymelfenig 1999).

2.3.2 Field and Laboratory Analyses

We collected invertebrate and sediment data in July and August 2010 and 2011 at the Jago, Okpilak/Hulahula, and Canning river deltas as part of a shorebird feeding study to determine the spatial distribution and abundance of invertebrates. We used a stratified random sampling framework with a grid of 250-m x 250-m cells that covered all available shorebird feeding habitat at each of the three delta study areas. A sample was collected from a random location in each grid cell. The spatial scale of the study was determined during 2009 on the Jago Delta when we sampled invertebrates at a 50-m scale and 400-m scale. The 250-m scale we selected to conduct the remainder of the study is comparable to similar studies in the Wadden Sea (Kraan et al. 2010), and sufficiently sampled the invertebrate patches we observed.

We collected samples across the grids at each delta during three periods: early (21 July – 1 August), mid- (1 – 8 August), and late season (10 – 22 August). Sampling during three periods allowed us to investigate temporal change in invertebrate abundance. These periods split the shorebird migration period into three approximately equal parts. All sampling occurred in areas accessible to feeding shorebirds, which were locations with water depths ≤ 5 cm and up to the tundra edge of the delta mudflat. If water depth at a sample location was > 5 cm it was not sampled during that session; a second random location within each grid square was sampled instead. The opportunity to sample two locations inside each grid square improved our sample coverage. At each sample location we collected an invertebrate and sediment core and recorded water depth to the nearest cm if present. The invertebrate core was collected with a PVC corer (1/100 m^2) pushed in the sediment to 5-cm depth (volume = 501.2 cm^3). We sifted the core through a 500-µm sieve and stored the macroinvertebrates and residual sediment in a plastic jar with 70% alcohol for preservation. The sediment core was obtained using a 50-cc syringe barrel. The syringe plunger was pushed in the sediment 5 cm (volume = 24.5 cm^3), and the sample was stored in a Whirl-pac® and frozen as soon as possible. All samples were shipped back to the University of Alaska Fairbanks for analysis.

We sorted invertebrate samples by taxa to the family level when possible. We identified samples to a higher taxonomic level than family when individuals were difficult to identify and were rare or the taxonomic level met the ecological level of interest as a shorebird food item (Table 2.1). Nematoda were not counted in 2010 because they are not considered a shorebird food, but were quantified in 2011. We counted individuals in the invertebrate core and extrapolated this to m^2 (± S.E.) to get an abundance estimate. The percent occurrence estimate

was calculated as the number of cores where the taxa was present divided by the total number of cores for that sampling session x 100.

Sediment core samples were weighed and dried at 65°C for 48 hrs to a constant weight to determine the percent moisture by weight. We also subsampled two 0.1-g samples into foil cups that were analyzed using a TruSpec Carbon/Nitrogen Determinator® to calculate a percentage by weight for total carbon and nitrogen. After these small portions were removed from the larger sediment sample, the remaining sample was used to determine the sample's grain size. Grain size measurements were conducted using different methods each year. In 2010 the sediment sample was weighed, suspended in water using a mixer, and then the sand was allowed to settle, which takes 40 seconds. After 40 seconds the solution containing the silt and clay portion was decanted leaving the sand, which was sifted using a 46-µm sieve to make sure all of the silt and clay were removed. Then after drying once more, the sample was weighed a final time to determine percent sand. We used the percentage silt/clay determined by 100 - sand. In 2011, after the subsamples for carbon and nitrogen were taken, the remaining sample was suspended in 100 ml of 70% hydrogen peroxide (H_2O_2) for 48 hrs to remove any organic material. The silt/clay portion was removed using a 63-µm sieve. Both the sand and silt/clay portions were dried to constant mass.

We also determined stable isotopic (^{13}C and ^{15}N) values for macroinvertebrate samples collected on the delta and nearby terrestrial tundra ponds. Samples of the dominant taxa were collected opportunistically from areas where they were present during past sampling using a core and sieve, and then were frozen as soon as possible. Soft-bodied taxa were dried at 65°C for 48 hrs to a constant weight and then the sample was homogenized and weighed into aluminum capsules. Taxa with a calcified exoskeleton were immersed in 2 M HCL for 24 hrs, rinsed in

deionized water, dried at 65°C for 48 hrs until constant weight was achieved; the sample was homogenized and weighed into aluminum capsules. Samples were analyzed at the Alaska Stable Isotope Facility (University of Alaska Fairbanks) using continuous flow stable isotope-ratio mass spectrometry in a Costech ECS4010 Elemental Analyzer (Costech Scientific, Valencia, CA) and Finnigan Delta Plus XP isotope ratio mass spectrometer through the Conflo III interface (Thermo-Finnigan, Bremen, Germany). We report our results in delta (δ) notation ‰ relative to the international standard (^{13}C = Viennna PeeDee Belemnite; ^{15}N = atmospheric nitrogen) using the equation: $\delta^{13}C = [R_{sample}/R_{standard}) - 1] \times 1{,}000$ with R representing the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Laboratory standards (peptone) were run with samples, and using the standard deviation of replicate measurements the analytical error was estimated to be $< \pm 0.2\%$.

2.3.3 Species Diversity, Distribution, and Statistical Analyses

Taxa and occurrence We calculated diversity indices using data from 2011 to compare the invertebrate communities among the three study deltas, using both Simpson's and Shannon's log base 10 diversity indices and evenness (Krebs 1989). Data from 2011 were selected because we had better detection of rare species that year. We are uncertain if the low number of rare species in 2010 was due to observer bias or a lack of rare species. We used both diversity indices because the Simpson's index reduces bias of rare species, while Shannon's index reduces bias of abundant species, but both indices increase with the number of species detected (Krebs 1989). Because we made identifications to different taxonomic levels, we have to assume that each taxon at our sites has only one family, which is the lowest taxonomic level of the analysis.

Invertebrate abundance We developed models using the statistical program R version 2.15.2 (R Development Core Team 2013) to evaluate the effect of site, year, session, and environmental factors on invertebrate abundance. We created linear mixed-effects restricted maximum

likelihood (REML) models using the R library lmerTest (Kuznetsova et al. 2013) and used stepwise model selection using backwards elimination of non-significant factors that were then further evaluated for fit. The dependent variable was invertebrate abundance of Chironomidae and Oligochaeta modeled respectively, which were the only two taxa with a significant sample size for this analysis. Random variables included factor variables for year, session, and delta, as well as interactions between these three variables. Chironomidae were only modeled for the Jago and Okpilak/Hulhula deltas because they were not present at the Canning. Fixed variables included delta; spatial variables latitude and longitude; and continuous variables for nitrogen, carbon, water depth, moisture, and percent silt/clay. We started with a full model containing the interaction "delta x longitude x water depth x moisture x silt/clay" and the other variables as non-interactive terms, based on past experience from modeling invertebrate populations in benthic habitats. We tested model and variable diagnostics using the variance inflation factor in the R library car (Fox et al. 2013) and Q-Q plots and residual plots in the lme4 library (Bates et al. 2013). Significance was set at $\alpha \leq 0.05$.

Invertebrate Distribution We used kriging to determine invertebrate distribution using the R library geoR (Ribeiro and Diggle 2013). Kriging is a geostatistical technique that uses the spatial variance between pairs of sample points to model the predicted values from each sample location, which is then extrapolated across the study area (Fortin and Dale 2005). We created a variogram using an exponential model, fit the model, and projected the model as a predictive map. Kriging maps were created for each year, sampling session, and major taxa combination, which allowed us to infer some natural history characteristics for these taxa.

We used Moran's I to calculate the spatial extent of invertebrate patches with R library spatial (Ripley 2013) for each year, sample session, and major taxa combination. Moran's I is a

spatial parameter that describes the spatial autocorrelation of a dataset by distance class (Fortin and Dale 2005). Moran's I can also be used to interpret patch size as a linear distance across the patch.

Isotopes We used MANOVA in R to test for differences between isotopic values of invertebrates collected in delta (marine) and tundra pond (terrestrial) habitats from three ponds in tundra habitat < 2 km from the Jago Delta. We calculated trophic level for invertebrates using a fractionation coefficient of 3.4‰ (Dunton et al. 2012), and the equation: $TL(POM) = \delta^{15}N_{Consumer} - \delta^{15}N_{POM}/ 3.4 + 1$ (Iken et al. 2010). The variable TL = trophic level and POM = particulate organic matter, which is the base measurement for $\delta^{15}N$ in the food chain.

2.4 Results

2.4.1 Taxa and Occurrence

We collected samples at 247, 525, and 487 sites over two years (2010 and 2011) on the Canning, Okpilak/Hulahula, and Jago Deltas respectively. Salinity and water temperature were similar at the Jago and Okpilak/Hulahula (Fig. 2.2), and most values were near zero with patches of saline water near gaps in the barrier islands. The Canning had higher salinity values and lower temperatures (Fig. 2.2) because of the proximity of this delta to an outlet to the ocean. Overall, we collected 18 taxa: 11 freshwater, 3 marine, 3 terrestrial, and one taxon that inhabits all habitats. Indices of diversity and evenness were highest at the Jago and lowest at the Canning (Fig. 2.3).

There were just six taxa that regularly occurred in our samples: Oligochaeta, Chironomidae, Tipulidae, Amphipoda, Chaetiliidae, and Spionidae (Table 2.2); however, these taxa were not found in every delta. For example, Chironomidae larvae were never observed at the Canning, although a few adults were present, despite the fact that they were sometimes the

most common taxa at other deltas. Tipulidae larvae were only found on one occasion at the Canning, but were common at the other two deltas. Spionidae were common at the Canning, uncommon at the Okpilak/Hulahula, and never found at the Jago. For each delta, annual variation for invertebrate occurrence was similar between 2010 and 2011 (Table 2.2), and there were no discernable patterns in occurrence observed within years for the Jago and Okpilak/Hulahula. The Canning tended to have fewer invertebrates in the early and mid-season periods, but invertebrate occurrence, especially for marine invertebrates, increased in the late season period. Overall, marine invertebrates were more prominent at the Canning compared to the other two deltas where freshwater invertebrates dominated.

2.4.2 Invertebrate Abundance

We determined invertebrate abundance at all three deltas for each year and sampling session (Table 2.3). Environmental variables were sampled for each invertebrate sample location at each delta (Fig. 2.2 and 2.4). In summary, Jago and Okpilak/Hulahula had similar sediment environmental characteristics, but the Canning had four times higher salinity and carbon values and tended to be cooler and drier on average than the other two sites. Chironomidae and Oligochaeta were the only two taxa common enough to make visual comparisons across years and sessions and to model abundance (Tables 2.4 and 2.5). There was a significant interaction between the random temporal variables year and session for both Chironomidae ($p < 0.05$; Table 2.4) and Oligochaeta ($p = 0.04$; Table 2.5). In the Chironomidae regression model the spatial variable Latitude was significant with a positive effect ($p < 0.001$), but spatial variables were not significant in the Oligochaeta model. The fixed environmental variables related to resources (total carbon and nitrogen) were not significant model predictors for either Chironomidae or Oligochaeta abundance. However, environmental variable interactions for moisture were

significantly positive (delta:moisture $p = 0.003$; silt:moisture $p = 0.011$) for Chironomidae, but negative (delta:moisture $p < 0.001$) for Oligochaeta (Tables 2.4 and 2.5).

2.4.3 Invertebrate Distribution

Spatial maps demonstrated consistent distribution, but varying abundance patterns across the spatial domain, which we were able to relate to invertebrate life history. Kriged maps of all invertebrates combined indicate invertebrate distributions were generally similar among years with core patches found on the edges and middle of the Jago delta, but abundance within patches varied (Fig. 2.5). We saw similar consistency in patches at the other deltas but were limited in our ability to present all of the data. The kriged abundances for some taxa were quite variable within the delta and among survey session, with abundances increasing later in the season (Fig. 2.6). Seasonally patches of Tipulidae larvae expanded from terrestrial tundra origins as summer progressed, while patches of Chironomidae larvae expanded from east to west. In contrast, Oligochaeta were consistently found in the same patches throughout the season.

Moran's I estimates of patch size for all invertebrates combined and individual taxa were 400 – 600 m. Almost all estimates were ≈ 400 m except there were a few estimates of ≈ 600 m measured for the Okpilak/Hulahula.

2.4.4 Stable Isotopes

With one exception noted below, freshwater and marine taxa collected on Beaufort Sea deltas had average $\delta^{13}C$ values ranging from -19.8 to -24.2‰, compared to organisms collected on tundra ponds on the Jago Delta that had more depleted mean $\delta^{13}C$ signatures ranging from -31.7 to -36.2‰; the separation of carbon isotope values between deltas and terrestrial wetlands fell between $\delta^{13}C$ -25‰ and - 27‰ (Fig. 2.7, Table 2.6). There was a significant difference in the $\delta^{13}C$ and $\delta^{15}N$ isotopic signature between delta and terrestrial samples ($p < 0.001$). Although

Culicidaea were collected on the delta, they had a strong terrestrial signature ($\delta^{13}C$ -31.0‰); we collected them on deltas as adults, but they likely had just hatched and migrated from nearby tundra ponds. The mean nitrogen isotopic signature for delta invertebrates ranged from $\delta^{15}N$ 1.3 to 6.6‰, and based on a trophic step fractionation of 3.4‰, delta consumers likely fall within two trophic levels, assuming that the $\delta^{15}N$ values for ultimate carbon sources on the deltas fall between 0 and 3‰ (Dunton et al 2012; Fig. 2.7). *Saduria* was the only taxon that spanned multiple trophic levels ($\delta^{15}N$ 4.7‰ and 8.7‰), reflecting the opportunistic feeding behavior of this invertebrate.

2.5 Discussion

2.5.1 Taxa and Occurrence

The fauna of the Beaufort Sea river deltas (70°N) are comparably more depauperate than the faunal communities of river deltas at more boreal latitudes (Lees et al. 1979, 1980; Powers et al. 2002). Taxa found at coastal sites of the Gulf of Alaska in southcentral Alaska (Copper River Delta, Port Valdez, and Cook Inlet at ~60°N) included Amphipoda, Chironomidae, and Polychaeta, but at most sites the dominant group was *Macoma* in the family Tellinidae (Lees et al. 1979, 1980; Powers et al. 2002). Although we did not find adult bivalves at our study sites, we found bivalve larva in a few locations (Baguley, unpublished data). *Macoma* and other bivalves were found in a nearby lagoon at 4.5 m depth providing a source population for young-of-the-year bivalves found on the mudflats (Dunton et al. 2012). In high arctic regions, ice drove community dynamics of intertidal areas including Spitsbergen (near 78°N) where all marine benthic invertebrates except Nematoda disappeared each winter (Weslawski and Szymelfenig 1999) and in the Canadian high Arctic (65°N-70°N), which had reduced or no macroinvertebrate benthic community in solid ice zones (Dale et al. 1989).

Previous studies have attributed the absence of marine fauna in the Beaufort Sea intertidal to the damaging physical disturbances of ice scour (Crane 1974, Feder and Schamel 1976, Gutt 2001). However, while ice scour likely contributes to the loss of relatively large metazoans, the multiple generations of freshwater dipteran larvae indicate that they survive total freezing of the intertidal and that such disturbances do not permanently eliminate all macroinvertebrates from the sediments. At the nearby Mackenzie Delta, scouring was less common at water depths < 2 m, perhaps because the entire water column is frozen at this depth (Hill et al. 2001). The lack of dynamic tides in lagoons on the Beaufort coast may also minimize scouring, although on Baffin Island intertidal fauna did survive in areas where tidal fluctuations prevented freezing to the bottom (Dale et al. 1989).

Freezing of the water column and sediments that annually kills some taxa during the winter, as observed on Spitsbergen and Baffin Island, likely drives the low diversity in marine invertebrates in Beaufort Sea deltas. There is considerable evidence that marine invertebrates survive at depths where freezing to the bottom is prevented (Dale et al. 1989, Dunton et al. 2012). Hard-shelled taxa like bivalves, periwinkles, and barnacles in hard bottom environments can withstand freezing temperatures to -10° C (Ellis and Wilce 1961, Gutt 2001), but bivalves dwelling in soft sediments do not survive freezing (Gutt 2001). Freezing is lethal to Amphipoda, Spionidae, and Chaetiliidae as well (Weslawski and Szymelfenig 1999), but these species can recolonize the intertidal each year from nearby lagoons (Zajac 1991, Drolet et al. 2013), where source populations can escape freezing (Dale et al. 1989, Weslawski and Szymelfenig 1999).

Our observations have theoretical applications as well. Strong disturbances that exceed a community's resilience (Boesch and Rosenberg 1981) will have a negative effect on invertebrate occurrence. Also, the intermediate disturbance hypothesis predicts highly disturbed areas will

have lower species diversity (Huston 1979). Annual freezing of Beaufort Sea intertidal habitats is a strong disturbance that exceeds the resilience of some taxa with the effect of reduced species diversity. Likewise, invertebrate occurrence at high Arctic deltas on Spitsbergen was low. Only one taxa was found at a similar depth as our sites (Wlodarska-Kowalczuk et al. 2007), and another study found four to nine taxa in samples collected at unknown depths at six different deltas (Weslawski and Szymelfenig 1999). In the Canadian high Arctic on Baffin Island macroinvertebrate taxa were few to absent (Dale et al. 1989). Lower species diversity is due to greater disturbance in shallow water habitat (Kendall 1996) and the lack of resistance and resilience in marine species to freezing (Boesch and Rosenberg 1981). Thus, Beaufort Sea intertidal habitats are populated with pioneering marine species that recolonize the benthos annually.

Unlike marine invertebrates, freshwater invertebrates are capable of surviving freezing events within the sediment (Strathdee and Bale 1998, Danks 2007). Beaufort delta sediments probably freeze all the way through to the underlying permafrost (Walker 1998), thus the strategy of burrowing deep into sediments to escape the ice is not possible. Chironomidae (Danks 1971, Andrews and Rigler 1985), Oligiochaeta (Andrews and Rigler 1985), and Tipulidae (Pritchard 1983) survive freezing events through freeze tolerance and supercooling (reviewed by Danks 1971, Strathdee and Bale 1998). Another strategy to withstand freezing events is seen in Chironomidae; they may withstand the mechanical stresses due to changes in sediment structure with ice crystal formation during freezing events by burrowing into fine silt/clay sediments (Danks 2007). Indeed, we found that Chironomidae abundance was associated with fine sediments. This finding is important as climate change will likely alter delta sediments; fine grain sediment accretion will decrease as glaciers in the Brooks Range disappear

in the next 50-75 years (Nolan et al. 2011). A final adaptation to this cold and variable environment is found in the order Diptera including Chironomidae, which has a population consisting of multiple generations (MacLean and Pitelka 1971, Butler 1982, Danks 2007). This trait is thought to increase persistence of a population in harsh environments in the event that one generation is unsuccessful (MacLean 1975).

2.5.2 Invertebrate Abundance

Environmental extremes like dessication, freezing, and predation and other factors in large part determine the survival and vertical distribution of intertidal biota (Anderson 1983). For deltas that have little vertical relief, the fauna still reflect habitat heterogeneity, food availability, exposure to predators, and physical dynamics. We investigated the association between invertebrates and some environmental variables by testing interactions between water depth, moisture, and fine sediments and found they were important predictors of Chironomidae and Oligochaeta abundance. In comparison, inundation time and fine sediment grain size were positively correlated with invertebrate abundance in other studies (Yates et al. 1993, Powers et al. 2002, Kraan et al. 2010), but they did not investigate interactions. The significant interactions in the present study indicate that associations between abundance and environmental variables may be more complex than previously reported. Sediment grain-size is usually a covariate with physical dynamics such that finer sediments persist in areas with reduced dynamics (Naidu and Mowatt 1983, Naidu and Klein 1988). Here, due to freezing, low tidal influences, and reduced available carbon due to glacial sediments (Wlodarska-Kowalczuk and Pearson 2004, Hood and Scott 2008) the complexity of environmental interactions may be greater.

2.5.3 Invertebrate Distribution

Survival strategies preventing freshwater invertebrates from freezing allow them to survive on the deltas, but we propose that freezing also plays an important role in shaping invertebrate distribution. For example, we found the distribution of Oligiochaeta was constant from one year to the next and within a season, but patches were small and habitat may be limited due to the frozen sediment in winter. In contrast, Chironomidae distribution increased across the mudflats as the summer progressed suggesting that in areas where populations were negatively impacted by freezing, they were able to recolonize through the summer. Tipulidae larvae radiated from the tundra's edge with increasing abundance over the summer coupled with a spread from the shore towards the water. Tipulidae adults lay eggs in south-facing tundra slopes, which collect heat early in the summer helping to initiate egg hatching (MacLean 1975, Pritchard 1983). Tipulidae pupae and adults were very rare in our samples, suggesting that these life stages occur outside delta habitats. Tipulidae may migrate out onto deltas during the larval stage to feed, but then migrate back to upland tundra to pupate and finish their life cycle. Their tracks stretching for meters are common on the sediment surface. If this is a true migration by this taxon, then future research should address how these insects return to specific habitats during different life stages, and how the linkages between the marine and terrestrial environments enhances survival in the delta.

2.5.4 Isotopic Analysis Trophic Community

The macroinvertebrate community of Beaufort Sea deltas was composed of two life history strategies, one marine and one with terrestrial freshwater origins. We hypothesized that these two groups would consume food from different carbon sources, with one reflecting a marine signature and the other a terrestrial signature. However, our data did not support this

hypothesis: the range in $\delta^{13}C$ values for biota with similar $\delta^{15}N$ was the same regardless of the life history strategy of the taxa, which reflects the assimilation across the delta of marine or terrestrial carbon sources, or some mixture of the two. Our values are similar to those from the same species collected in Beaufort lagoons at ≤ 4.5 m depth (*Spio filicornis* -22.3‰, *Gammarus setosus* -23.4‰, and *Saduria entomon* -21.0‰; Dunton et al. 2012). We did not observe a gradient of enriched to depleted $\delta^{13}C$ values from the lagoon to the delta found by researchers on the Colville River delta (Craig et al. 1984), but these three deltas are comparably tiny compared to the massive delta of the Colville. The isotopic signatures we observed from resident delta fauna were distinctly more ^{13}C enriched than values observed in nearby tundra ponds, although a representative of the Culicidae collected on the delta showed it had just emigrated from a tundra pond base on its $\delta^{13}C$ value of -31.5‰. Our data clearly show the importance of terrestrial sources of carbon, also demonstrate the dependence of the benthic fauna on marine sources of carbon. Our recent work (Dunton, unpublished data) has shown that sediment chlorophyll concentrations range up to 204 mg m^{-2}, which would provide a significant source of labile carbon for the benthic infauna on the tidal flats of the these deltas. In addition, concentrations of various phaeopigments reveal very active grazing of the sediment microalgae by benthic metazoans (Dunton, unpublished data). This information, along with the evidence from stable isotope data, indicate that the food webs of the high latitude river deltas may shift from allocthonous (terrestrial) to autogenous (marine benthic microalgae) sources of carbon once the deltas become ice-free.

2.5.5 Study Implications

The disturbance-prone intertidal habitats we surveyed had fewer taxa than temperate areas, and furthermore, the marine taxa were generalists. However, some of the freshwater taxa

were specialists that could be impacted by climate change including changes in sediment aggregation, erosion from storm surges, and sea level rise. Sediment accretion in river deltas of the Beaufort Sea may be greater now than in the past due to increased melting of glaciers in the Brooks Range (Hinzman et al. 2005, Nolan et al. 2011). However, sediment transport will decline in the next 50-75 years when glacial ice disappears and is replaced by annual snow fields (Nolan et al. 2011). Changes in sedimentation rates will likely transform sediment structure by increasing grain size, a change that could further affect some invertebrates, especially those associated with more fine-grain sediments (e.g. the Chironomidae).

Glacial sediments in particular have unique characteristics due to high ion exchange and low carbon content that will impact the invertebrate community from the bottom up with more available carbon if glacial sediments are absent (Naidu and Klein 1988, Hood and Scott 2008). In our samples we find a four-fold increase in total carbon measurements between glacial fed and non-glacial fed deltas (Fig. 2.4). Storm surge frequency is increasing on the Beaufort Sea coast (Hinzman et al. 2005, Walsh 2008), and storm surges are often observed first-hand (Crane 1974, Martin 1983). However, the effects of these events on deltaic habitats are unknown, although the invasion of sea water likely increases salinity in brackish water areas and increases erosion. Sea level rise could also change delta habitats, but with little knowledge of the extent of the change in the Arctic Ocean it is difficult to predict actual impacts to deltas (Proshutinsky and Bourke 2001). Regardless, expectations are that sedimentation rates will not counter sea level rise (Weston 2014).

Resource development for oil could also impact coastal delta areas; offshore drilling has already begun within 7 km of the Canning River delta, and more development along the coast is expected. Oil spills adversely affect invertebrate communities (Percy 1976, Miller et al. 1986,

Feder et al. 1990, Peterson et al. 2003). The full impact of an arctic oil spill is currently unknown, but biodegradation of oil in Arctic conditions is being researched to prepare for spill response and assess Arctic conditions (McFarlin et al. 2011, Prince et al. 2013). Our data provide baseline information on pre-development invertebrate communities of the Beaufort Sea that could help assess impacts and restore habitats to their previous condition. Our data also provide insights into resilience of these communities. The absence of many marine fauna on the delta suggests source populations from the lagoon. In the event of a large but temporally short disturbance, the perturbation may have limited effects as marine fauna repopulate rapidly on an annual basis. Freshwater fauna would likely recolonize from source populations in the river.

In conclusion, invertebrate communities on the Beaufort Sea coast are dominated by disturbances unique to high latitudes, rather than those of lower latitude deltas in Alaska, largely due to the impact of annual freezing. Beaufort Sea deltas are important sources of food for wading birds and migrating estuarine fishes during the summer. The availability of food resources is a product of the survival of various freshwater invertebrate species that are resilient to freezing and the active annual migration and colonization of invertebrates from protected marine invertebrate "source" populations in adjacent lagoons. Because of their contributions to estuarine ecology as well as their contributions to migrating birds, future research of lagoon ecosystems on the Beaufort Sea should include intertidal habitats and the freshwater taxa we found, which will require new sampling regimes. Our exploration of arctic deltas has allowed us to suggest mechanisms for survival in this environment, and future studies can test these mechanisms and associations we have highlighted.

2.6 Acknowledgements

We thank the many dedicated field technicians who helped collect samples. The National Fish and Wildlife Foundation, Bureau of Ocean Energy Management, US Fish and Wildlife Service Arctic National Wildlife Refuge, and the Arctic Landscape Conservation Cooperative funded this study. We had logistical support from the Arctic National Wildlife Refuge, USGS Alaska Cooperative Fish and Wildlife Research Unit, Institute of Arctic Biology, and Manomet Conservation Sciences. We had lab support from the Mark Wipfli aquatic invertebrate lab, Alaska Stable Isotope Facility, University of Alaska Forestry Soil Sciences Lab, and the Alaska Monitoring and Assessment Program. We are also thankful to the Kaktovik Inupiat Corporation for letting us conduct research on their lands and the people of the village of Kaktovik for their help and friendship. We thank C. Davis and two anonymous reviewers for their thoughtful review of this manuscript. Any use of trade product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the United States government.

2.7 References

Anderson, F.E. 1983. The Northern Muddy Intertidal: Seasonal factors controlling erosion and deposition - a review. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 143–159.

Andres, B.A. 1989. Littoral zone use by post-breeding shorebirds on the Colville River Delta, Alaska. M.S. Thesis. Columbus, Ohio: Ohio State University.

Andrews, D., and F.H. Rigler. 1985. The effects of an Arctic winter on benthic invertebrates in the littoral zone of Char Lake, Northwest Territories. *Canadian Journal of Zoology* 63: 2825–2834.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2013. Package lme4. https://github.com/lme4/lme4/ http://lme4.r-forge.r-project.org/.

Boesch, D.F., and R. Rosenberg. 1981. Response to stress in marine benthic communities. In *Stress Effects on natural Ecosystems*, ed. G. W. Barrett and R. Rosenberg, 179–200. Chichester, UK: John Wiley & Sons Ltd.

Brown, S., S. Kendall, R. Churchwell, A. Taylor, and A.-M. Benson. 2012. Relative shorebird densities at coastal sites in the Arctic National Wildlife Refuge. *Waterbirds* 35: 546–554.

Butler, M.G.G. 1982. A 7-year life cycle for two Chironomus species in arctic Alaskan tundra ponds (Diptera: Chironomidae). *Canadian Journal of Zoology* 60: 58–70.

Connors, P.G., and R.W. Risebrough. 1977. Shorebird dependence on Arctic littoral habitats. In Environmental Assessment of the Alaskan Continental Shelf (Annual Reports of Principal Investigators), Volume 3: 402-524: Outer-continental Shelf Environmental Assessment Program, Anchorage, Alaska.

Craig, P.C. 1984. Fish use of coastal waters of the Alaskan Beaufort Sea: a review. *Transactions of the American Fisheries Society* 133: 265–282. doi:10.1577/1548-8659(1984)113<265.

Craig, P.C., W.B. Griffiths, S.R. Johnson, and D.M. Schell. 1984. Trophic dynamics in an Arctic lagoon. In *The Alaskan Beaufort Sea: Ecosystems and Environments*, ed. P. W. Barnes, D. M. Schell, and E. Reimnitz, 347–380. Orlando, FL: Academic Press, Inc.

Crane, J.J. 1974. Ecological studies of the benthic fauna in an arctic estuary. M.S. Thesis. Fairbanks, Alaska: University of Alaska, Fairbanks.

Dale, J.E., A.E. Aitken, R. Gilbert, and M.J. Risk. 1989. Macrofauna of Canadian arctic fjords. *Marine Geology* 85: 331–358. doi:10.1016/0025-3227(89)90159-X.

Danks, H.V. 1971. Overwintering of some north temperate and arctic Chironomidae. *The Canadian Entomologist* 103: 1875–1910.

Danks, H.V. 2007. How aquatic insects live in cold climates. *The Canadian Entomologist* 139: 443–471.

Drolet, D., M.R.S. Coffin, M.A. Barbeau, and D.J. Hamilton. 2013. Influence of intra- and interspecific interactions on short-term movement of the Amphipod *Corophium volutator* in varying environmental conditions. *Estuaries and Coasts* 36: 940–950.

Dunton, K.H., S.V. Schonberg, and L.W. Cooper. 2012. Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. *Estuaries and Coasts* 35: 416–435.

Dunton, K.H., T. Weingartner, and E.C. Carmack. 2006. The nearshore western Beaufort Sea ecosystem: circulation and importance of terrestrial carbon in arctic coastal food webs. *Progress In Oceanography* 71: 362–378. doi:10.1016/j.pocean.2006.09.011.

Ellis, D.V., and R.T. Wilce. 1961. Arctic and subarctic examples of intertidal zonation. *Arctic* 14: 224–235.

Feder, H.M., A.S. Naidu, and A.J. Paul. 1990. Trace element and biotic changes following a simulated oil spill on a mudflat in Port Valdez, Alaska. *Marine Pollution Bulletin* 21: 131–137.

Feder, H.M., and D. Schamel. 1976. Shallow-water benthic fauna of Prudhoe Bay. In *Assessment of the Arctic Marine Environment: Selected Topics*, 329–359. University of Alaska Fairbanks.

Fortin, M-J., and M. Dale. 2005. *Spatial Analysis*. Cambridge: Cambridge University Press.

Fox, J., S. Weisberg, D. Adler, D. Bates, G. Baud-Bovy, S. Ellison, D. Firth, et al. 2013. Package car. https://r-forge.r-project.org/projects/car/.

Fry, B. 2006. *Stable Isotope Ecology*. New York: Springer Verlag.

Gutt, J. 2001. On the direct impact of ice on marine benthic communities, a review. *Polar Biology* 24: 553–564.

Hill, P.R., C.P. Lewis, S. Desmarais, V. Kauppaymuthoo, and H. Rais. 2001. The Mackenzie Delta: sedimentary processes and facies of a high-latitude, fine-grained delta. *Sedimentology* 48: 1047–1078.

Hinzman, L.D., N.D. Bettez, W.R. Bolton, F.S. Chapin, M.B. Dyurgerov, C.L. Fastie, B. Griffith, et al. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change* 72: 251–298.

Hood, E., and D. Scott. 2008. Riverine organic matter and nutrients in southeast Alaska affected by glacial coverage. *Nature Geoscience* 1: 583–587. doi:10.1038/ngeo280.

Huston, M. 1979. A general hypothesis of species diversity. *The American Naturalist* 113: 81–101.

Iken, K., B. Bluhm, and K.H. Dunton. 2010. Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 57. Elsevier: 71–85.

Kendall, M.A. 1996. Are Arctic soft-sediment macrobenthic communities impoverished ? *Polar Biology* 16: 393–399.

Kraan, C., G. Aarts, J. van der Meer, and T. Piersma. 2010. The role of environmental variables in structuring landscape-scale species distributions in seafloor habitats. *Ecology* 91: 1583–1590.

Krebs, C.J. 1989. *Ecological Methodology*. New York, NY: Harper Collins Publishers.

Kruse, J.A. 1991. Alaska Inupiat subsistence and wage employment patterns: understanding individual choice. *Human Organization* 50: 317–326.

Kuznetsova, A., P.B. Brockhoff, and R.H.B. Chris-Tensen. 2013. Package lmerTest. http://cran.r-project.org/web/packages/lmerTest/lmerTest.pdf.

Lees, D.C., D.E. Erikson, W. Driskell, and D.E. Boettcher. 1979. *Intertidal and Shallow Subtidal Biological Studies: Valdez Port Expansion Project*. U.S. Department of Commerce, NOAA, OCSEAP Report, Anchorage, Alaska.

Lees, D.C., J.P. Houghton, D.E. Erickson, W. Driskell, and D.E. Boettcher. 1980. *Ecological studies of intertidal and shallow subtidal habitats in lower Cook Inlet, Alaska*. U.S. Department of Commerce, NOAA, OCSEAP Final Report, Anchorage, Alaska.

Levin, S.A., and R.T. Paine. 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences of the United States of America* 71: 2744–2747.

MacGinitie, N. 1959. Marine Mollusca of Point Barrow, Alaska. *Proceedings of the U.S. National Museum* 109: 59–208.

MacLean, S.F. 1975. Ecological adaptations of tundra invertebrates. In *Physiological Adaptation to the Environment*, ed. F. John Vernberg, 269–300. New York: Intext Educational Publishers.

MacLean, S.F., and F.A. Pitelka. 1971. Seasonal patterns of abundance of tundra Arthropods near Barrow. *Arctic* 24: 19–40.

Marsh, P., and T. Schmidty. 1993. Influence of a Beaufort Sea storm surge on channel levels in the Mackenzie Delta. *Arctic* 46: 35–41.

Martin, P.D. 1983. Bird use of arctic tundra habitats at Canning River Delta, Alaska. M.S. Thesis. University of Alaska, Fairbanks. Fairbanks, Alaska.

McFarlin, K.M., R.A. Perkins, W.W. Gardiner, J.D. Word, and J.Q. Word. 2011. Toxicity of physically and chemically dispersed oil to selected arctic species. *International Oil Spill Conference Proceedings* 2011: 1–7.

Mikan, C.J., J.P. Schimel, and A.P. Doyle. 2002. Temperature controls of microbial respiration in arctic tundra soils above and below freezing. *Soil Biology and Biochemistry* 34: 1785–1795.

Miller, M.C., J.R. Stout, and V. Alexander. 1986. Effects of a controlled under-ice oil spill on invertebrates of an arctic and a subarctic stream. *Environmental Pollution Series A, Ecological and Biological* 42: 99–132.

Moitoret, C.S. 1983. Bird use of arctic coastal shorelines at Canning River Delta, Alaska. M.S. Thesis. University of Alaska Fairbanks, Fairbanks, Alaska.

Naidu, A.S., and L.H. Klein. 1988. Sedimentation processes. In *Environmental Studies in Port Valdez, Alaska: A Basis for Management*, ed. D. G. Shaw and M. J. Hameedi, 69–92. Berlin: Springer-Verlag.

Naidu, A.S., and T.C. Mowatt. 1983. Sources and dispersal patterns of clay minerals in surface sediments from the continental-shelf areas off Alaska. *Geological Society Of America Bulletin* 94: 841–854.

Newbury, T.K. 1983. Under landfast ice. *Arctic* 36: 328–340.

NOAA. 2010. NOAA Tide Predictions: Flaxman Island 2010. Retrieved from http://tidesandcurrents.noaa.gov/get_predictions.shtml?year=2010&stn=7292+Kodiak&secstn=Flaxman+Island&thh=-0&thm=57&tlh=-0&tlm=28&hh=*0.08&hl=*0.09&footnote=.

NOAA. 2014. NOAA: National Climate Data Center Average monthly temperature 2010-2014. National Climate Data Center.

Nolan, M., R. Churchwell, J. Adams, J. McClelland, K.D. Tape, S. Kendall, A. Powell, K. Dunton, D. Payer, and P. Martin. 2011. Predicting the impact of glacier loss on fish, birds, floodplains, and estuaries in the Arctic National Wildlife Refuge. In *Observing, Studying, and Managing for Change*, ed. C. Nicolas Medley, Glenn Patterson, and Melanie J. Parker, 49–54. Reston, Virginia: U.S.G.S. Scientific Investigations Report 2011- 5169.

Norton, D., and G. Weller. 1984. The Beaufort Sea: background, history, and perspective. In *The Alaskan Beaufort Sea: Ecosystems and Environments*, ed. P. W. Barnes, D. M. Schell, and E. Reimnitz, 3–22. Orlando: Academic Press, Inc.

Percy, J.A. 1976. Responses of arctic marine crustaceans to crude oil and oil-tainted food. *Environmental Pollution* 10: 155–162.

Peterson, C.H., S.D. Rice, J.W. Short, D. Esler, J.L. Bodkin, B.E. Ballachey, and D.B. Irons. 2003. Long-term ecosystem response to the Exxon Valdez oil spill. *Science* 302: 2082–2086.

Powers, S.P., M.A. Bishop, J.H. Grabowski, and C.H. Peterson. 2002. Intertidal benthic resources of the Copper River Delta, Alaska, USA. *Journal of Sea Research* 47: 13–23.

Prince, R.C., K.M. McFarlin, J.D. Butler, E.J. Febbo, F.C.Y. Wang, and T.J. Nedwed. 2013. The primary biodegradation of dispersed crude oil in the sea. *Chemosphere* 90. Elsevier Ltd: 521–526.

Pritchard, G. 1983. Biology of Tipulidae. *Annual Review of Entomology* 28: 1–22.

Proshutinsky, A., and R.H. Bourke. 2001. Sea level rise in the Arctic Ocean. *Geophysical Research Letters* 28: 2237–2240.

R Development Core Team. 2013. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Ribeiro, P.J., and P.J. Diggle. 2013. Package geoR. http://www.leg.ufpr.br/geoR.

Ripley, B. 2013. Package spatial. http://www.stats.ox.ac.uk/pub/MASS4/.

Strathdee, A.T., and J.S. Bale. 1998. Life on the edge: insect ecology in arctic environments. *Arctic* 43: 85–106.

Taylor, A.R., A.N. Powell, D.A. Nigro, and S.J. Kendall. 2010. Distribution and community characteristics of staging shorebirds on the northern coast of Alaska. *Arctic* 63: 451 – 467.

Walker, H.J. 1998. Arctic deltas. *Journal of Coastal Research* 14: 718–738.

Walsh, J.E. 2008. Climate of the arctic marine environment. *Ecological Applications* 18: S3–S22.

Weslawski, J.M., and M. Szymelfenig. 1999. Commumity composition of tidal flats on Spitsbergen: consequence of disturbance? *Biogeochemical Cycling and Sediment Ecology* 59: 185–193.

Weston, N.B. 2014. Declining sediments and rising seas: an unfortunate convergence for tidal wetlands. *Estuaries and Coasts* 37: 1–23.

Wiens, J.A. 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. In *The Ecological Consequences of Environmental Heterogeneity*, ed. M. J. Hutchings, E. John, and A. J. A. Stewart, 9–32. Oxford: British Ecological Society.

Wlodarska-Kowalczuk, M., and T.H. Pearson. 2004. Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). *Polar Biology* 27: 155–167. doi:10.1007/s00300-003-0568-y.

Wlodarska-Kowalczuk, M., M. Szymelfenig, and M. Zajiczkowski. 2007. Dynamic sedimentary environments of an arctic glacier-fed river estuary (Adventfjorden, Svalbard). II: meio- and macrobenthic fauna. *Estuarine, Coastal and Shelf Science* 74: 274–284.

Yates, M.G., J.D. Goss-Custard, S. McGrorty, K.H. Lakhani, S. dit Durell, R.T. Clarke, W.E. Rispin, et al. 1993. Sediment characteristics, invertebrate densisites and shorebird densisites on the inner banks of the Wash. *Journal of Applied Ecology* 30: 599–614.

Zajac, R. 1991. Population ecology of *Polydora ligni* (Polychaeta: Spionidae). I. Seasonal variation in population characteristics and reproductive activity. *Marine Ecology Progress Series* 77: 197–206.

Table 2.1. Taxonomic list of invertebrates sampled at Beaufort Sea deltas, 2010 – 2011. Taxa are underlined at the level at which we conducted the analysis. Superscript [F] = freshwater taxa, [S] = saltwater taxa, [B] = commonly found in both salt and freshwater, and [T] = terrestrial taxa.

Phylum	Class	Order	Family	Genus	species
Nematoda[B]					
Annelida					
	Clitellata				
		Oligochaeta[F]			
	Polychaeta				
		Canalipalpata			
			Spionidae[S]		
				Spio	*S. filicornis*
Arthopoda					
	Maxillipoda				
		Copepoda[F]			
	Malacostraca				
		Amphipoda[S]			
			Lysianassidae		
				Orchomene	
			Pontoporeiidae		
				Pontoporeia	*P. femorata*
		Isopoda			
			Chaetiliidae[S]		
				Saduria	*S. entomon*
	Arachnida				
		Araneae[T]			
		Trombidiformes			
			Hydrachnidiae[F]		
	Entognatha				
		Collembola[F]			
	Insecta				
		Hymenoptera[T]			
		Hemiptera			
			Cicadellidae[T]		
		Plecoptera			
			Capniidae[T]		
		Diptera			

Table 2.1 Continued

	Chironomidae[F]	
		Diplocladius
		Chironomus
	Tipulidae[F]	
		Ormosia
	Culicidae[F]	
	Empididae[F]	
	Ephydridae[F]	
	Ceratopugonidae[F]	

Table 2.2. The percentage that each taxa contributed to invertebrate occurrence for each delta and season on the Beaufort Sea coast. Percentage is the number of cores where taxon was present divided by total cores collected for that period x 100. Nematodes were only quantified in 2011. Species in the Other category include those species that only occurred once within a season and delta, including Capniidae, Cicadellidae, Arachnida, Copepoda, Empididae, Ephydridae, Hydrachnidia, and Hymenoptera. The "**" represents no detection of a taxa.

	Canning 2010			Canning 2011		
	Early Season	Mid Season	Late Season	Early Season	Mid Season	Late Season
Amphipoda	4.4	4.6	26.3	**	**	18.1
Chaetiliidae	4.4	**	5.0	**	**	**
Chironomidae	4.4	4.6	**	3.7	**	1.4
Culicidae	**	**	**	3.7	**	**
Oligochaeta	13.0	4.6	27.5	7.4	34.2	34.7
Spoinidae	**	**	11.2	**	4.9	8.3
Tipulidae	**	**	**	**	**	1.4
Other	**	**	**	7.4	**	1.4
No Invertebrates	73.9	86.4	30.0	77.8	61.0	33.3
	Jago 2010			Jago 2011		
Amphipoda	3.3	5.2	6.5	2.3	3.0	10.5
Chaetiliidae	1.1	1.7	1.1	**	**	2.2
Chironomidae	30.0	24.1	33.7	19.3	24.0	23.9
Culicidae	2.2	3.5	**	**	1.0	**
Nematoda	**	**	**	2.3	5.0	4.5
Oligochaeta	14.4	10.3	21.7	25.0	19.0	16.4
Tipulidae	21.1	20.7	17.4	15.9	12.0	10.5
Other	**	**	1.1	2.3	2.0	1.5
No Invertebrates	27.8	34.5	18.5	33.0	34.0	30.6
	Okpilak/Hulahula 2010			Okpilak/Hulahula 2011		
Amphipoda	3.2	**	**	1.3	2.4	3.6
Chaetiliidae	5.4	**	5.3	**	0.8	1.2
Chironomidae	39.8	37.2	42.7	30.3	30.4	23.8
Culicidae		1.1	**	**	**	**
Nematoda	**	**	**	1.3	5.6	**
Oligochaeta	8.6	7.0	13.3	23.7	22.4	10.1
Spionidae	**	**	**	**	**	25.0
Tipulidae	4.3	9.3	13.3	7.9	3.2	1.8

Table 2.2 Continued

Other	1.1	**	**	2.6	4.8	6.6
No Invertebrates	36.6	46.5	25.3	32.9	30.4	1.2

Table 2.3. Abundance estimates (mean ± S.E.) of macroinvertebrate taxa from the Canning, Jago, and Okpilak/Hulahula River deltas. Measurements are abundance m^{-2}. The "**" represents no detection of a taxa.

	Canning 2010			Canning 2011		
	Early Season	Mid Season	Late Season	Early Season	Mid Season	Late Season
Amphipoda	8.70 ± 8.70	4.55 ± 4.55	172.5 ± 59.11	**	**	158.93 ± 85.80
Chaetiliidae	4.35 ± 4.35	**	5.00 ± 5.00	**	**	**
Chironomidae	4.35 ± 4.36	**	10.00 ± 10.00	3.70 ± 3.70	**	3.57 ± 3.57
Collembola	**	**	**	7.40 ± 7.40	**	**
Culicidae	**	**	**	3.70 ± 3.70	**	**
Ephydridae	**	**	**	**	**	1.79 ± 1.79
Nematoda	**	**	**	**	**	3.57 ± 3.57
Oligochaeta	69.57 ± 56.73	9.09 ± 9.09	490.00 ± 139.75	55.56 ± 48.43	943.59 ± 293.58	876.79 ± 294.37
Spionidae	**	**	52.50 ± 22.29	**	5.13 ± 3.58	28.57 ± 15.65
Tipulidae	**	**	**	**	**	1.79 ± 1.79
	Jago 2010			Jago 2011		
Amphipoda	4.30 ± 2.61	31.67 ± 24.18	28.57 ± 22.12	2.90 ± 2.03	3.80 ± 2.16	69.47 ± 31.47
Arachnida	**	**	**	**	1.27 ± 1.27	**
Capniidae	**	**	**	1.45 ± 1.45	**	1.05 ± 1.05
Chaetiliidae	1.08 ± 1.08	1.67 ± 1.67	1.10 ± 1.1.0	**	**	3.16 ± 1.80
Chironomidae	235.48 ± 68.66	185.00 ± 70.86	575.82 ± 123.54	108.70 ± 36.86	496.20 ± 141.77	538.95 ± 118.45
Cicadellidae	**	**	1.10 ± 1.10	**	**	**
Collembola	**	**	**	1.45 ± 1.45	**	1.05 ± 1.05
Copepoda	**	**	**	**	**	1.05 ± 1.06
Culicidae	2.15 ± 1.51	3.33 ± 2.34	**	**	1.27 ± 1.27	**
Ephydridae	**	**	**	**	1.27 ± 1.28	**
Nematoda	**	**	**	2.90 ± 2.90	21.52 ± 12.70	10.53 ± 4.61
Oligochaeta	211.83 ± 100.35	15.00 ± 7.45	205.49 ± 62.83	349.28 ± 132.56	311.39 ± 203.78	543.16 ± 206.86
Tipulidae	36.56 ± 9.64	56.67 ± 22.09	51.65 ± 15.18	40.58 ± 12.44	40.51 ± 15.02	72.63 ± 26.79
		Okpilak/Hulahula 2010			Okpilak/Hulahula 2011	
Amphipoda	8.70 ± 6.68	**	**	1.72 ± 1.72	4.12 ± 2.50	17.32 ± 11.02

Table 2.3 Continued

Capniidae	1.09 ± 1.09	**	**
Chaetiliidae	6.52 ± 3.01	**	5.33 ± 2.61
Chironomidae		226.08 ± 70.27	143.18 ± 60.07
Collembola	**	**	**
Copepoda	**	**	**
Culicidae	1.09 ± 1.09	**	**
Empididae	**	**	**
Hydrachnidia	**	**	**
Hymenoptera	**	**	**
Nematode	**	**	**
Oligochaeta	130.43 ± 85.62	161.36 ± 115.78	109.33 ± 57.83
Spionidae	**	**	**
Tipulidae	5.43 ± 2.83	25.00 ± 13.45	17.33 ± 5.49

**	2.06 ± 2.06	
**	1.03 ± 1.03	2.36 ± 1.76
228.00 ± 56.14	198.28 ± 80.74	217.53 ± 48.98
3.45 ± 3.45	1.03 ± 1.03	178.74 ± 42.05
**	3.09 ± 3.09	1.57 ± 1.57
**	**	0.79 ± 0.79
**	1.03 ± 1.03	**
**	1.03 ± 1.04	**
1.72 ± 1.72	1.03 ± 1.05	**
1.72 ± 1.73	59.79 ± 34.33	**
613.79 ± 224.10	857.73 ± 245.00	68.50 ± 29.27
**	**	1339.37 ± 305.66
31.03 ± 21.04	10.31 ± 6.63	7.09 ± 5.61

Table 2.4. Effects of environmental factors on Chironomidae abundance on Beaufort Sea deltas based on a linear model in which we found a significant interaction between the random temporal variables year and session ($p < 0.05$). All variables for the best model are shown and only significant random variables are reported. Significance of fixed factors was used in a stepwise model selection using backwards elimination of non-significant factors.

Random Factors			Fixed Factors				
Variable	Variance	S.D.	Variable	Estimate	S.E.	*t*-value	*p*-value
Year:Session	0.00	0.06	Intercept	-629.60	128.40	-4.91	0.000
Residual	0.18	0.42	Latitude	8.99	1.83	4.91	0.000
			Delta	-1.09	0.22	-4.95	0.000
			Moisture	-0.01	0.01	-1.32	0.188
			Silt	-0.01	0.01	-2.38	0.018
			Delta:Moisture	0.03	0.01	2.96	0.003
			Moisture:Silt	0.00	0.00	2.56	0.011

Table 2.5. Effects of environmental factors on Oligochaeta abundance on Beaufort Sea deltas based on a linear mixed model in which we found a significant interaction between the random temporal variables year and session ($p = 0.04$). All variables for the best model are shown and only significant random variables are reported. Significance of fixed factors was used in a stepwise model selection using backwards elimination of non-significant factors.

Random Factors			Fixed Factors				
Variable	Variance	S.D.	Variable	Estimate	S.E.	*t*-value	*p*-value
Year:Session	0.01	0.07	Intercept	-0.77	0.27	-2.88	0.004
Residual	0.26	0.51	Delta	0.44	0.12	3.74	0.000
			Moisture	0.06	0.01	4.52	0.000
			Delta:Moisture	-0.02	0.01	-4.39	0.000

Table 2.6. Carbon and nitrogen isotopic values for benthic macroinvertebrates (mean ± SE) and the C/N ratio for corresponding samples collected from Beaufort Sea deltas and three tundra ponds < 2 km from the Jago Delta, 2010 – 2011.

	N	$\delta^{15}N$ (‰ ± SE)	$\delta^{13}C$ (‰ ± SE)	C:N (Moles/mole ± SE)
Delta				
Amphipoda	5	4.5 ± 0.3	-22.0 ± 0.7	5.6 ± 0.2
Chironomidae	2	3.0 ± 0.5	-22.3 ± 1.6	5.8 ± 0.4
Culicidae	1	3.3	-31.3	4.1
Oligiochaeta	1	5.2	-22.0	5.3
Saduria	2	6.6 ± 2.0	-19.8 ± 0.7	4.8 ± 0.1
Spionidae	2	5.1 ± 0.0	-24.2 ± 0.4	5.9 ± 0.0
Tipulidae	6	1.3 ± 0.4	-23.7 ± 0.1	5.8 ± 0.2
Tundra Ponds				
Anostraca	2	1.4 ± 0.0	-36.2 ± 0.6	4.1 ± 0.1
Chironomidae	6	1.7 ± 0.3	-31.6 ± 0.9	4.8 ± 0.1
Cladocera	1	0.2	-34.6	5.1
Coleoptera	3	2.6 ± 0.4	-31.8 ± 1.9	4.7 ± 0.4
Oligiochaeta	5	0.7 ± 0.2	-31.7 ± 0.9	4.7 ± 0.1
Ostracoda	1	0.8	-34.4	5.1
Plecoptera	1	1.1	-35.4	4.8

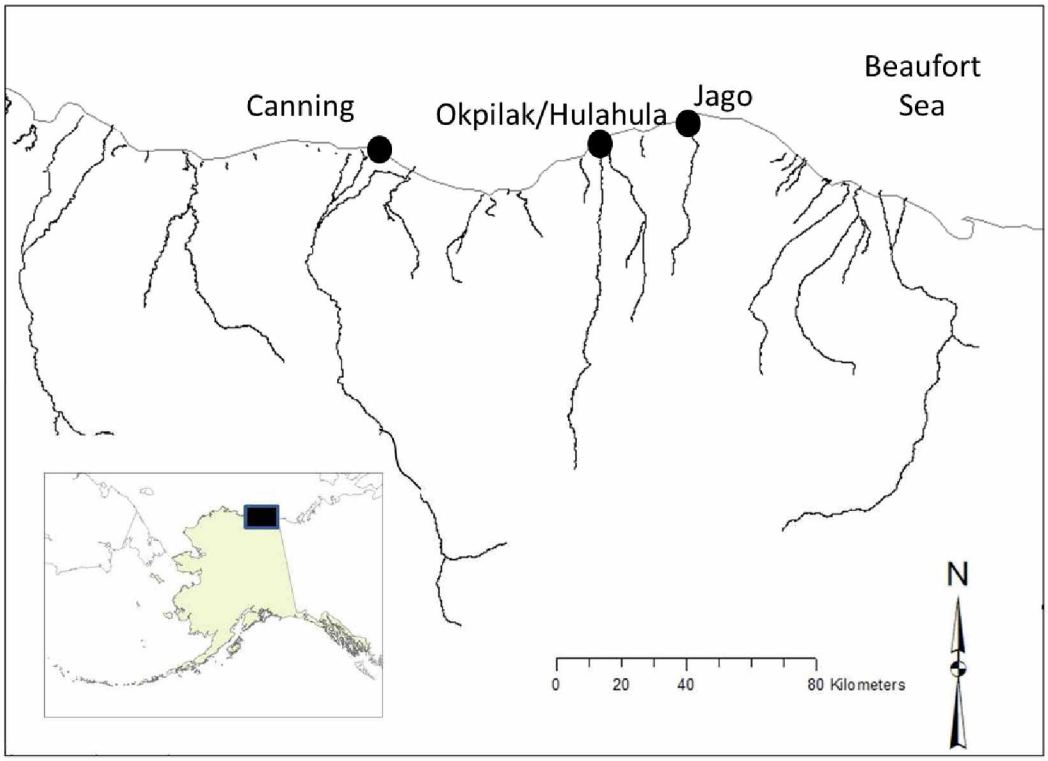

Figure 2.1. The location of the three river deltas that were sampled in this study from 2009 to 2011 in the Alaskan Beaufort Sea.

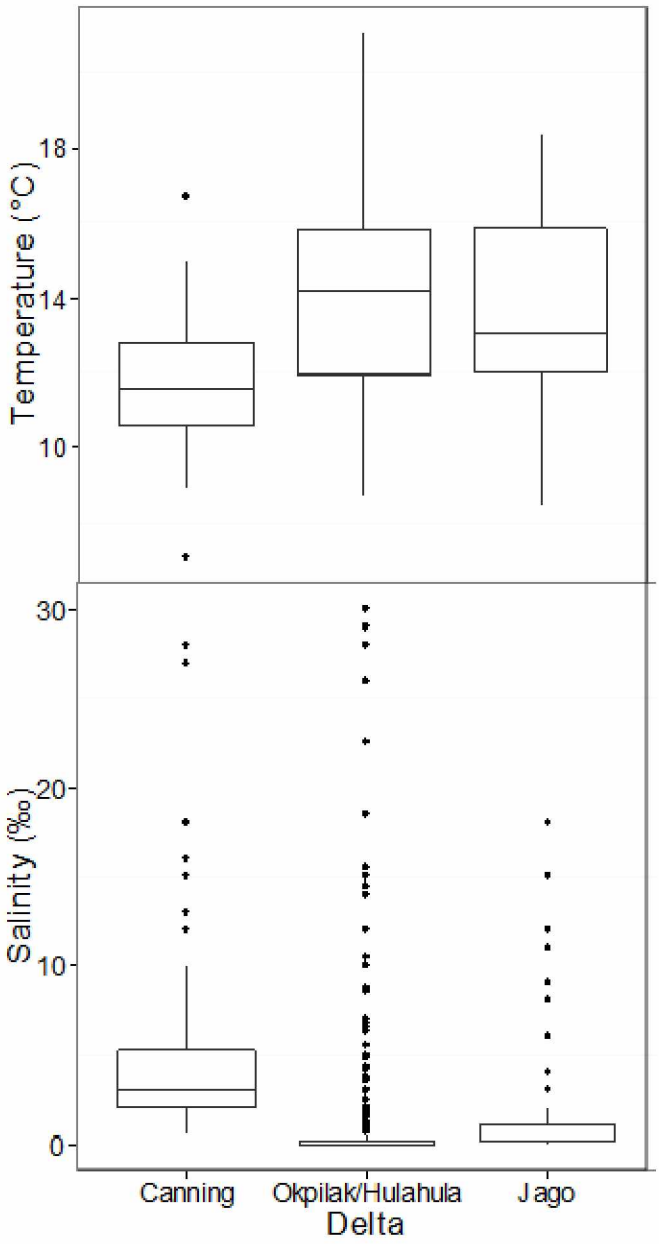

Figure 2.2. The mean salinity and temperature for each Beaufort Sea delta, 2010 – 2011. The box represents the first and third quartile, the whiskers represent one standard deviation, and the dots are outliers.

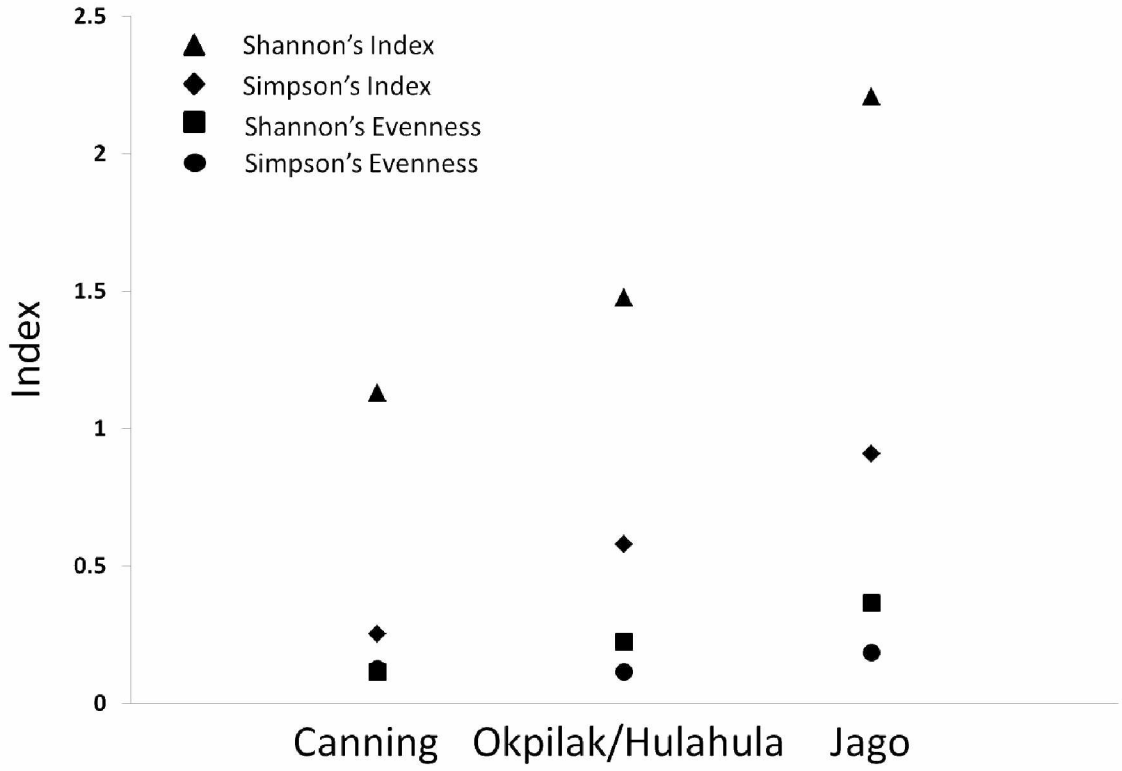

Figure 2.3. Shannon and Simpson's diversity indices and evenness for invertebrate taxa sampled on Beaufort Sea deltas 2011. Individuals were identified to the family level or assumed to contain one family if identified at a higher taxonomic level.

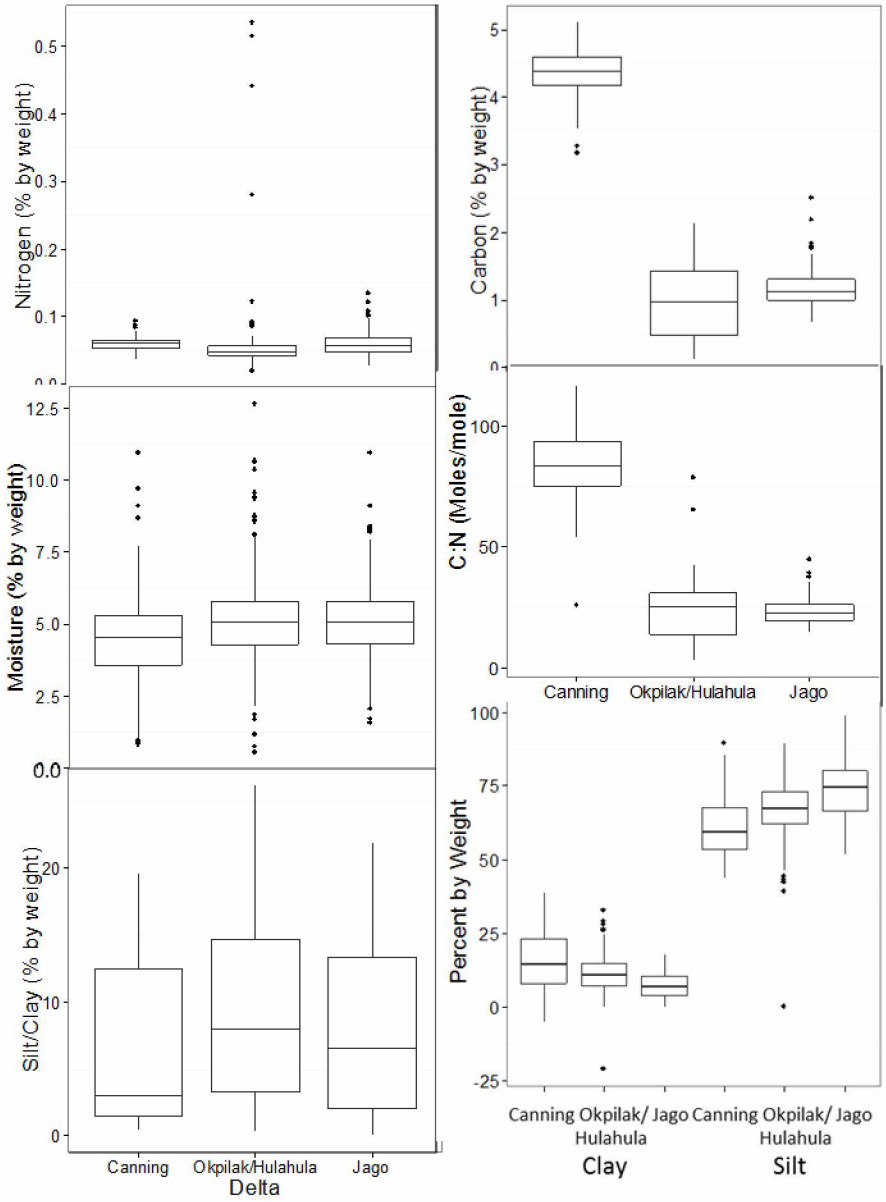

Figure 2.4. Sediment grain size with respect to the silt/clay fraction (bottom left panel), soil moisture, and C:N data from Beaufort Sea deltas, 2010 – 2011. The unquantified portion of the sample is sand. The proportion of clay or silt in the combined silt/clay fraction by weight fraction for each delta sediment sample is included (bottom right panel).

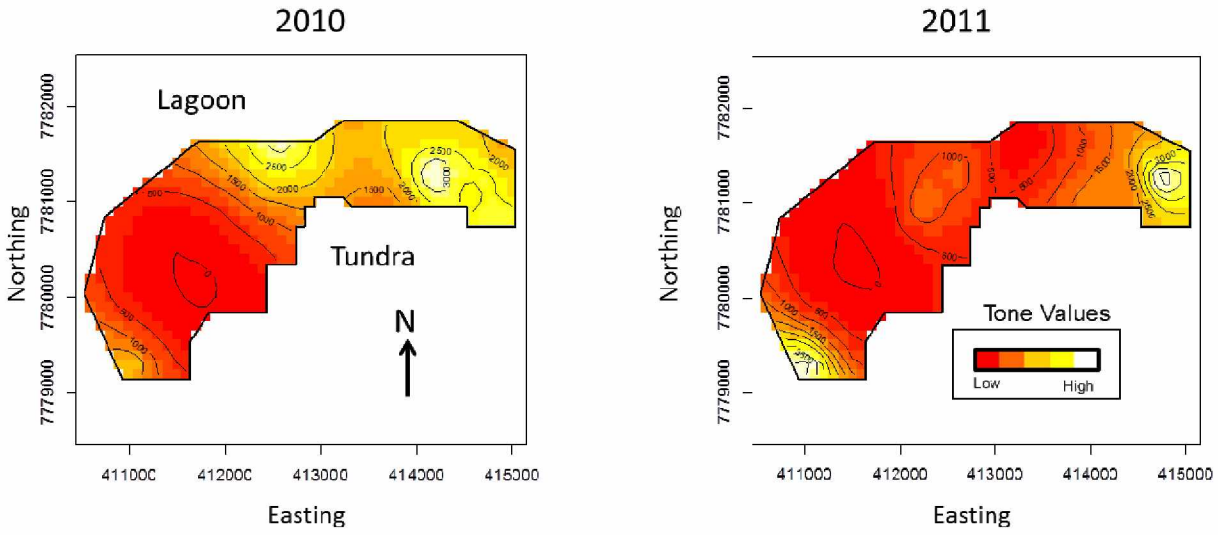

Figure 2.5. Predicted distribution of all invertebrate taxa combined during late-season sampling at the Jago River Delta 2010 – 2011.

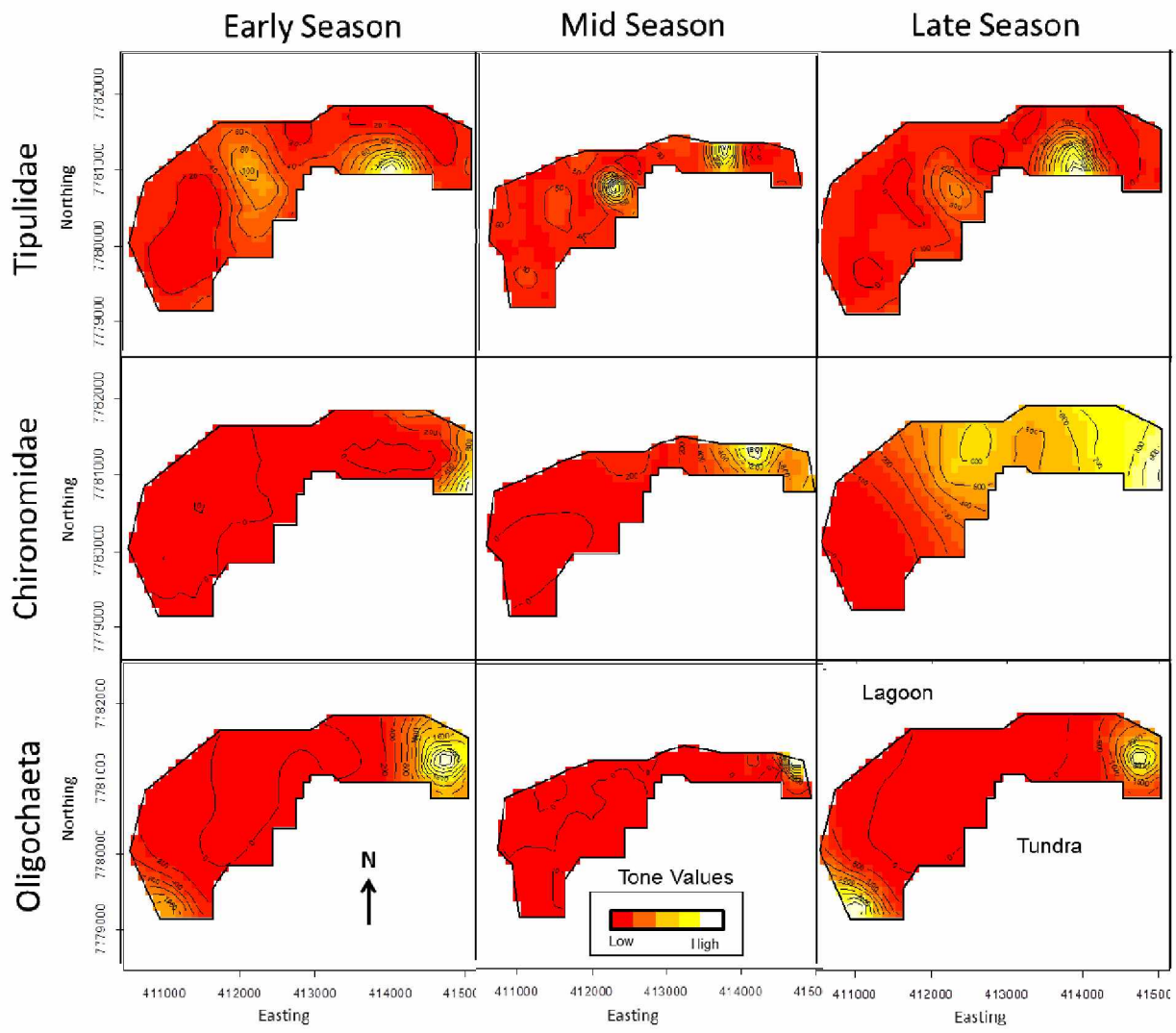

Figure 2.6. Predicted distribution of invertebrate taxa through three sampling periods (early = 21 July – 1 August, mid = 1 August – 8 August, late = 10 August – 22 August) at the Jago River Delta 2011. The area of the delta changes during the mid-season due to lower water levels during that period.

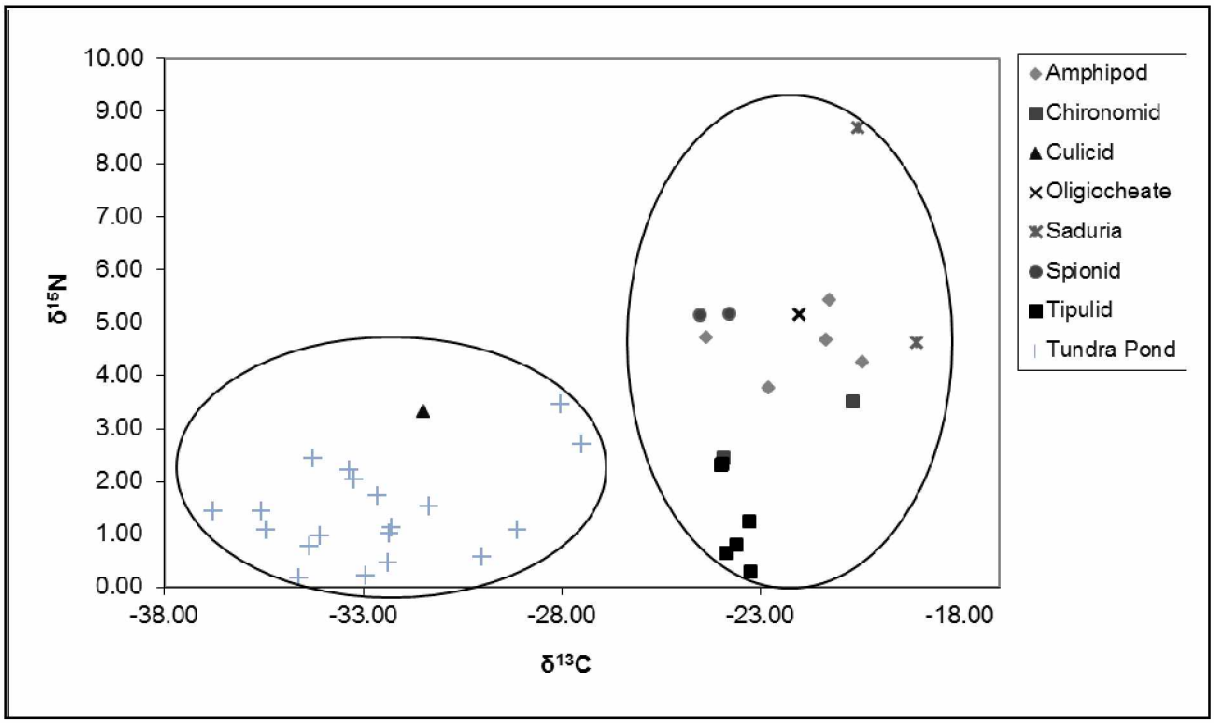

Figure 2.7. Stable isotopic values ($\delta^{15}N$ and $\delta^{13}C$) of the major invertebrate taxa found on Beaufort Sea deltas. Separate circles encompass all of the samples collected on the delta and within tundra ponds except for Culicidae, which were collected on the delta as adults that we believe had just migrated from nearby tundra ponds as reflected in their depleted $\delta^{13}C$ values.

3 The First Hop: Semipalmated Sandpiper Use of Beaufort Sea Deltas[1]

3.1 Abstract

The Semipalmated Sandpiper (*Calidris pusilla*) is one of the most common coastal migrants across northern North America, but populations in the East have recently suggested a drastic decline at stopover sites and wintering areas. Demographic information and stopover ecology research pertaining to the three populations of this species (Alaskan, central Canadian, and eastern Canadian) may provide evidence for the cause of decline in the eastern population while elucidating the potential for the decline to spread to the other populations. Our research determined the beginning of the fall migration (postbreeding period) of the Alaskan population, and we determined the importance of several delta mudflats on the Beaufort Sea coast to this migration. We sampled invertebrates, counted shorebirds, and captured Semipalmated Sandpipers to collect a blood sample for triglyceride and stable isotope analyses from three deltas along the northeastern coast of Alaska. We found Semipalmated Sandpiper numbers were associated with abundance of Chironomidae and Oligochaeta. The isotopic signature from blood plasma samples indicated birds switched from a diet of upland invertebrates to marine invertebrates as the migration season progressed. We tested for differences among the three deltas in habitat quality using blood plasma triglyceride level, which measures the fattening rate of birds, but found no differences. A stable isotope mixing model indicated shorebird diet was different at each delta, suggesting flexibility in shorebird diet allowing migrants to exploit abundant food resources. Our research demonstrates the importance of these river delta mudflats

[1] To be submitted to The Condor: Churchwell, R.T., S. Kendall, S.C. Brown, A.L. Blanchard, T.E. Hollmen, A.N. Powell. (XXXX). The first hop: Semipalmated Sandpiper use of Beaufort Sea deltas. Condor

at the beginning of the migration for the Alaskan Semipalmated Sandpiper population, and we are now able to speculate on how changes in this habitat including potential impacts of climate change or coastal development might impact this population. Future research focused on the Canadian populations will allow for a comparison among the populations that may lead to insights into eastern Canada's decline in Semipalmated Sandpipers.

3.2 Introduction

Semipalmated Sandpipers (*Calidris pusilla*) are the second most common species of shorebird breeding on the Arctic Coastal Plain (Brown et al. 2007, Johnson et al. 2007) and the most common species observed during fall migration on the Beaufort Sea coast of the Arctic National Wildlife Refuge (Brown et al. 2012). There are three populations of Semipalmated Sandpipers (Harrington and Morrison 1979): Alaskan, central Canadian, and eastern Canadian. In contrast to the extensive decline in the eastern Canadian population (Morrison et al. 1994), demonstrated by a 79% decrease in wintering counts between 1980 and 2011 (Morrison et al. 2012), the Alaskan population appears to be stable (Morrison et al. 1994, Gratto-Trevor et al. 2012b, Smith et al. 2012). The reason for the decline of Canadian, but not Alaskan populations is unknown; however, differences in migration routes and stopover sites may play a role. After breeding on the Arctic Coastal Plain, Alaskan birds move north to coastal habitats where they prepare for migration by foraging, then move from west to east along the Beaufort Sea coast (Connors and Risebrough 1977, Taylor et al. 2010). After crossing northern Alaska they migrate south through the central US and spend the winter from Ecuador to French Guiana and along the Pacific coast of South America (Harrington and Morrison 1979, Gratto-Trevor et al. 2012a). Birds that breed in central and eastern Canada stage at the Bay of Fundy and then migrate across the ocean to South America where they winter from Suriname to northern Brazil (Harrington and

Morrison 1979, Gratto-Trevor et al. 2012a); however, there are no published studies of post-breeding and early migratory movements for Canadian populations. Recently, light-level geolocators were deployed on Semipalmated Sandpipers across their breeding range (Stephen Brown, unpublished data) in order to better understand their migratory routes. Unfortunately, locations above the Arctic Circle are not obtained from this technology, and thus movements from breeding grounds to their first stopover sites cannot be detected (Egevang et al. 2010, Porter and Smith 2013). Differences in migration strategies and locations of stopover sites among the three populations may explain divergent population trajectories.

Migration strategies, with respect to distances flown between stopover sites, are often referred as "hop," "skip," and "jump" strategies (Piersma 1987, Warnock 2010). Migrants that "hop" are characterized by many short flights with more frequent short stops for refueling, "skip" migrants travel for intermediate distances and lengths-of-stay, and "jump" migrants fly thousands of miles with stops for refueling that last for weeks. Migration theory suggests that when food resources are variable from year to year, shorebirds tend to use a "hop" strategy by making shorter flights and using stopover sites for shorter times to minimize energy use (Skagen and Knopf 1994). Semipalmated Sandpipers migrating along the Beaufort Sea coast use a "hop" strategy, flying ≈ 100 km between stops and staying at stopover sites for an average of four days (Taylor et al. 2011). As a result, they have low energy demands for migration. Juvenile Semipalmated Sandpipers leaving the Arctic were observed to start the migration with low fat reserves (Lindstrom et al. 2002), which may allow for earlier migration and minimizes time in migration by allowing the birds to start sooner. Shorebirds typically spend the majority of the migration period at stop-over sites, and if they can move between sites with lower fat reserves then less time is allotted to accruing resources, which shortens the migration period overall

(Alerstam and Lindstrom 1990). However, there may be other energy demands on migrants that require such short flights, such as the continued physical growth of juvenile birds at the start of their first migration. The majority of migrant Semipalmated Sandpipers on the Beaufort Sea coast in fall are hatch-year birds and thus need to meet the energetic requirements for continued growth as well as migration; the drivers of their use of stopover sites on the first "hop" of fall migration are unknown.

On the Beaufort Sea coast, adult Semipalmated Sandpipers leave the breeding grounds on average 6 days earlier than juveniles and may migrate by a different route; it is unclear whether they extensively use coastal stopover sites before heading south (Taylor et al. 2010, Brown et al. 2012). Juvenile birds, however, first head north to coastal habitats before heading east and south on migration. The culmination of growth of juvenile sandpipers as migration begins may constitute a bottleneck in their annual cycle (Buehler and Piersma 2008). Differing migration strategies for adult versus juvenile sandpipers suggests that energy requirements for the two age groups are not the same. In addition, food resource availability often dictates use of stopover habitats as well as distribution of shorebirds across individual sites. Within sites, shorebirds are often distributed in proportion to available food resources (Beauchamp et al. 1997, Beauchamp and Ruxton 2008).

Shorebirds may be highly dependent on the abundance of one particular invertebrate species found at stopover sites; however, shorebird diets may be more diverse than originally thought. For example, Semipalmated Sandpipers were thought to feed almost exclusively on amphipods in the Bay of Fundy (Hicklin and Smith 1984), but with the use of stable isotope analysis, it was found that they also feed heavily on polychaete worms and biofilm (Quinn and Hamilton 2012). It is uncertain whether these food items were always in the diet but previously

undetected, or if there was a recent shift in shorebird diet. Diet composition is important because food preferences may be based on specific fatty acid compounds that prepare birds for migration (McWilliams et al. 2002). For example, amphipods contain high levels of omega 3 fatty acids, which in experiments on red-eyed vireos increased exercise performance (Pierce et al. 2005, Maillet and Weber 2006). While many studies suggest that shorebirds select food items according to their abundance (Skagen and Oman 1996), preferential selection may be beneficial and could also determine habitat use. Many factors may influence the quantity and quality of food selected however, and only a few preferences have been explored.

While food is a major factor, predation risk is often a more important predictor of stopover site selection (Ydenberg et al. 2002), distribution of birds on a mudflat (Pomeroy 2005), and abundance of birds at a site (Beauchamp 2009, 2010). Regardless of whether predators are present, birds may avoid areas up to 100 m from the edge of a mudflat due to the perception of risk (Pomeroy 2006, Pomeroy et al. 2006). Predation may also impact the timing of migration; predation pressure is lower if shorebirds start their migration before their major avian predators. For example, adult Semipalmated Sandpipers precede the eastern Canada Peregrine Falcon (*Falco peregrinus tundrius*) migration (Lank et al. 2003). Ultimately, shorebird migration is partially regulated by predation (Alerstam and Lindstrom 1990), but we know nothing of predator impacts to shorebird migration on the Beaufort Sea coast.

To determine relative use of delta mudflats along the Beaufort Sea coast and factors influencing abundance and distribution of shorebirds among and within these sites, we first quantified their use by hatch-year Semipalmated Sandpipers. We added a temporal component by quantifying differences among years and within three periods of fall migration (early, mid, and late). To relate use to food resources, we quantified availability of invertebrate taxa across

each delta during the same time periods. Because it was unknown whether shorebirds were feeding exclusively on delta mudflats on their first hop of migration, we used stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) to detect marine versus terrestrial signatures of invertebrate prey in relationship to their blood plasma. This allowed us to establish whether shorebirds were dependent on food derived from mudflat habitats for fueling their migratory movements. Then, to obtain an index of relative habitat quality among deltas, we used blood triglyceride levels to determine fattening rates (Williams et al. 1999, Guglielmo et al. 2002) of birds compared to invertebrate abundance at each site. We expected to find a positive relationship between invertebrate abundance, triglyceride levels, and shorebird abundance indicative of high-quality habitat (Ydenberg et al. 2002). Finally, we investigated the influence of perceived predation risk on shorebird distribution within sites by quantifying predator occurrence at each delta and estimating the amount of available predator-safe habitat. We predicted that deltas with more predators and less predator-safe habitat would support fewer shorebirds that had greater energy needs. Information on the feeding ecology of these birds will help us understand why we find indications of differential migration among adult and juvenile Semipalmated Sandpipers, as well as possibly providing insight into causes of decline in the eastern Canadian population and suggesting threats to the Alaskan population. The importance of these stopover sites is ultimately a determinant of several demographic variables; selection of delta mudflats may influence successful migration, annual survival, and fecundity through carry-over effects within a shorebird's annual cycle (Baker et al. 2004, Harrison et al. 2011).

3.3 Methods

3.3.1 Study Area

River deltas along the Beaufort Sea are part of a complex lagoon ecosystem, and are protected from marine influences by low barrier islands parallel to the coast. The islands regulate passage from the marine to the lagoon through inlets between the islands that are 10 – 50 m wide and 1 – 2 m deep. During summer months, these lagoons and the associated littoral zones of the deltas are warmer and less saline than the adjacent marine environment (Dunton et al. 2012). Lunar tides on the coast range from -6 cm to 24 cm and average 10.5 cm (NOAA 2010). The lunar tide height only contributes partially to water levels on the mudflats because of a substantial surge effect, which is the product of an interaction between the Beaufort Gyre that flows from east to west along Alaska's north coast (Norton and Weller 1984) and atmospheric pressure, wind speed, and wind direction (Martin 1983, Marsh and Schmidty 1993). The surge makes the water level unpredictable because it is derived from weather patterns; however, water level is also relatively constant because the lunar influence is minimal and weather patterns don't often change from day to day.

We established study sites at three of these river deltas, Canning, Okpilak/Hulahula, and Jago, in July and August (Fig. 3.1). The Jago delta is the farthest east and approximately 650 ha, the Okpilak/Hulahula is 20 km to the west (740 ha), while the smallest site, Canning, is another 60 km west (290 ha). All of the deltas have sand, silt, and clay sediments, but no gravels were sampled (Churchwell et al. 2015). At the Jago and Okpilak/Hulahula, salinity is zero for most of their perimeters except for small areas on their western ends. In contrast, ~ 25-50% of Canning's perimeter is saline (~12-20‰), depending on the prevailing ocean currents (Churchwell unpublished data).

3.3.2 Spatial and Temporal Patterns of Shorebirds

Shorebird counts were conducted between the third week in July as the nesting season finished and the third week in August when most of the Semipalmated Sandpipers had moved south. We surveyed shorebirds every three days at each of the three study deltas, and we counted birds across the entire delta with each survey. A 100- x 100-m grid was delineated using wooden lathe on each delta, and the species, number, and age of birds in each cell were recorded. A smaller scale was used than that used for invertebrate collection (described below) because it was not possible to visually quantify shorebirds within the larger invertebrate grid. Even though we had 24-hr daylight for much of the survey period, we counted birds starting in the mid-morning (around 9:00 AM) until we had covered the survey area, which took 6-8 hrs on the larger deltas. We did not count birds later in the evening because shorebird activity declined.

We present shorebird count data as total daily counts and densities that were not corrected for detection probability. Total counts, which are the raw number of birds counted, represent an estimate of the number of birds on the delta that day. We estimated density by dividing the total count by the area (ha) of the delta surveyed that day to standardize by delta size. We did not account for detection probability because other research has found a detection rate of 0.99 for shorebirds in this habitat (Brown et al. 2012).

3.3.3 Invertebrate Sampling

To determine spatial and temporal patterns of invertebrate abundance, we used a stratified random sampling framework, with a grid of 250-m x 250-m cells, which covered all available shorebird feeding habitat at each of the three study sites. The spatial scale of the grid was determined during 2009 on the Jago Delta, when we sampled invertebrates within both 50-m

and 400-m grids. We compared the variance in estimates of samples from these two scales and decided something intermediate (250 m) was most appropriate, as well as comparable to similar studies in the Wadden Sea (Kraan et al. 2009a).

To capture temporal patterns of invertebrate abundance and distribution, we collected samples at each delta during three time periods (sessions) corresponding with fall migration: early (21 July – 1 August), mid- (1 – 8 August) and late (10 – 22 August) 2010 and 2011. We only sampled areas with water depths ≤ 5 cm, which were accessible to feeding shorebirds. If water depth at a sample location was > 5 cm it was not sampled during that session; a second random location within each grid square was evaluated for water depth and sampled instead. If both locations were > 5 cm then the grid cell was not considered foraging habitat. We collected an invertebrate core and when water was present, recorded water depth to the nearest cm at each sample location. We used a PVC corer (1/100 m^2) pushed into the sediment to 5-cm depth (volume = 501.2 cm^3) to sample invertebrates. We sifted the core through a 500-µm sieve and stored preserved invertebrates and residual sediment in a plastic jar with 70% alcohol.

In the lab, we sorted invertebrate samples by taxa to the family level when possible. We identified samples to a higher taxonomic level than family when individuals were difficult to identify and were rare, or the taxonomic level met the ecological level of interest as a shorebird food item. Nematoda were not counted in 2010 because they are not considered a shorebird food, but were quantified in 2011 as part of another project. We counted individuals in the invertebrate core and extrapolated this to inverts m^{-2} (± S.E.) for each site and time period to get an abundance estimate.

Finally, we collected taxa for a stable isotope analysis to compare delta and upland tundra food items. We collected about five samples for the common taxa from each delta including all

taxa that were potential food items. Sampling was conducted opportunistically during other tasks. Larger invertebrates were sampled when they were observed on the mudflat, and smaller invertebrates were sampled with a core and sieve in areas where they were known to be common. We also sampled three upland tundra ponds within 2 km of the Jago Delta, collecting taxa similar to those found on the delta.

3.3.4 Bird Captures and Blood Sample Collection

To characterize fattening rates based on triglycerides and determine shorebird diet based on blood $\delta^{13}C$ and $\delta^{15}N$, we captured Semipalmated Sandpipers, using mist nets during two periods, early (23 July – 6 August) and late (8 – 20 August). These two sessions roughly separate the migration season into two equal sessions, but they are not the same time periods as the invertebrate sessions. Each bird was fitted with a USGS aluminum leg band. We recorded length of tarsus (mm) for standardizing body size, age based on plumage, mass (g), and fat score as covariates in triglyceride models. We also collected a 0.1-cc blood sample from the jugular using a 1.0-cc syringe and a 26 5/8 gauge needle < 20 minutes from capture, and recorded time of capture and time of bleed. Blood samples were stored chilled in a cooler and processed within six hours, and spun in a centrifuge at 6,000 rpm for 10 minutes to separate the blood from plasma. Plasma and red blood cells were stored separately in a liquid nitrogen cryoshipper (MVE liquid nitrogen freezer – Series SC 20/20) until laboratory analysis.

Isotopic analyses. The isotopic signature of food items was quantified to establish shorebird diet and compare it with plasma samples we collected from the birds. We determined stable isotopic ($\delta^{13}C$ and $\delta^{15}N$) values for invertebrate samples collected on delta mudflats and nearby terrestrial tundra ponds as described previously. Soft-bodied invertebrate taxa were dried at 65°C for 48 hrs until constant weight was achieved. Taxa with a calcified exoskeleton were immersed in 2 M

HCL for 24 hrs, rinsed in deionized water, and dried at 65°C for 48 hrs until constant weight was achieved. All dried samples were weighed into aluminum capsules for analysis (see below).

We also measured $\delta^{13}C$ and $\delta^{15}N$ isotopes on red blood cells and plasma from birds. We used blood cells (~ 1 month turnover rate) and plasma (~ 1 week turnover), to characterize diet on two different time scales (Hobson and Clark 1993). The separate parts of the blood were freeze dried and weighed into aluminum capsules that were then analyzed for stable isotope signatures.

Samples were analyzed for carbon and nitrogen isotopic signatures at the Alaska Stable Isotope Facility (University of Alaska Fairbanks) using continuous flow stable isotope-ratio mass spectrometry. A Costech ECS4010 Elemental Analyzer (Costech Scientific, Valencia, CA) was used with a Finnigan Delta Plus XP isotope ratio mass spectrometer through the Conflo III interface (Thermo-Finnigan, Bremen, Germany). We report our results in delta (δ) notation ‰ relative to the international standard (^{13}C = Viennna PeeDee Belemnite; ^{15}N = atmospheric nitrogen) using the equation: $\delta^{13}C = [R_{sample}/R_{standard}) - 1] \times 1{,}000$ with R representing the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Laboratory standards (peptone) were run with samples, and using the standard deviation of replicate measurements the analytical error was estimated to be $< \pm 0.2\%$.

Fattening rates. We measured triglycerides at the Alaska Sealife Center (Seward, Alaska) using an endpoint assay in a microplate spectrophotometer (Molecular Devices LLC Spectramax Plus 384) set at 540 nm wavelength. We ran the triglyceride reagent (Sigma #T2499) and free glycerol reagent (Sigma #F6428) assays in 96 well microplates using 5 µL of plasma. We calculated the triglyceride level by subtracting our measurement of free glycerol from the total triglyceride measurement. We ran quality control samples comparing measurements of a known sample standard (Sigma #G7793) each day (coefficient of variation = 0.8 - 13.1 among

standards) and then analyzed the results in a regression correlation to the standard with an expected correlation $R^2 \approx 1.0$ (all R^2 were > 0.99).

3.3.5 Index of Avian Predators

Avian predators were also counted during shorebird surveys. Predators counted included Merlin (*Falco colombarius*), Peregrine Falcon, Gyrfalcon (*F. rusticolus*), Northern Harrier (*Circus cyaneus*), Long-tailed (*Stercorarius longicaudus*), Parasitic (*S. parasiticus*), and Pomarine jaegers (*S. pomarinus*). We derived a predator index by dividing the time a predator was recorded by the hours of daily observation. The estimate was multiplied by 100 resulting in predators/100 hrs, which is commonly reported in the literature.

3.3.6 Analyses

Shorebirds and invertebrates. To investigate relationships between shorebird and invertebrate abundance, we used a linear mixed-effects restricted maximum likelihood (REML) model in package lmerTest (Kuznetsova et al. 2013) in Program R version 2.15.2 (R Development Core Team 2013). The Canning did not have enough data to run in this model so we only included data from the Jago and Okpilak/Hulahula. Random variables, which allowed the intercept to vary with each factor, included session (time period) and year. Fixed variables, which do not vary in their intercept, included easting and northing (Universal Transverse Mercator coordinate system), delta, and abundance of Amphipoda, Oligochaeta, Chironomidae, and Tipulidae. The final model was determined using backwards selection, and included all variables with $\alpha \leq 0.05$.

Isotopic analysis. We tested for differences in isotopic values for blood samples collected early- and late-season. We used MANOVA in Program R to simultaneously test for differences in nitrogen and carbon (N= 57); significance was set at $\alpha \leq 0.05$. To explore the proportion of individual taxa in shorebird diet using the isotopic signatures of plasma and available

invertebrate taxa, we used a Bayesian mixing model diet analysis in MixSIAR (Semmens and Ward 2014). For this analysis, both invertebrate and plasma values were corrected for bias due to differences in lipid concentration using the C:N ratio (Post et al. 2007). Because invertebrate diversity differed at the three study sites, we ran the analysis twice. First we included Tipulidae, Chironomidae, Amphipoda, and Oligochaeta, which were available food items at Jago and Okpilak/Hulahula. The second analysis included Spionidae and dropped Chironomidae for Canning.

Triglyceride and mass analyses. To determine relationships between triglyceride levels and shorebird mass among deltas, we used ANCOVA in Program R (N=170). We included delta, invertebrate abundance at the banding location, year, session, banding time, handling time (duration), tarsus (mm), and fat score as potential explanatory variables.

Predators. We tested for differences in the index of predators among deltas (N=115), years, and sessions using ANOVA in Program R with significance set at $\alpha \leq 0.05$. For each of the mudflat sites we delineated areas sandpipers avoid and where predators have cover to make an attack using a 100-m buffer (Pomeroy et al. 2006) along the tundra edge of the mudflat. Then we ranked each delta by the percentage of area where sandpipers were relatively safe.

3.4 Results

3.4.1 Shorebird Abundance

We found large numbers of shorebirds used the deltas; however, there was variability in delta use and timing of migration. Of the Semipalmated Sandpipers observed at our study sites, 98% were hatch-year birds, and we never captured an adult. Timing of fall migration for all age classes began around 20 July and was mostly over by 24 August along the eastern Beaufort Sea. Peak migration occurred between 27 July and 7 August at the Jago, with 3,000 - 4,000 birds at

the peak, 2009-2012 (Fig. 3.2a). However, timing of peak abundances varied among sites. For example, in 2011 we counted 4,000 birds at Okpilak/Hulahula on 12 August, whereas we observed a similar peak of 4,000 birds at Jago almost two weeks earlier (Fig. 3.2b). Canning had a similar pattern as Okpilak/Hulahula, but the peak in bird numbers was < 1,000 birds.

3.4.2 Invertebrate Abundance

Among years, abundance of common taxa was relatively similar at each site with the exception of Oligochaeta. Abundances of Oligochaeta were higher in 2011, and within 2011 increased at least two-fold during the late time period at Okpilak/Hulahula and much more during the mid and late periods at the Canning (Fig. 3.3). In addition, invertebrate communities differed among the sites (Table 3.1). The community at Canning was the most dissimilar, characterized by more marine-associated taxa, including small but abundant patches of Spionid polychaete worms and almost no Chironomidae or Tipulidae. Okplilak/Hulahula was characterized by a wide variety of taxa, but Chironomidae and Oligochaeta were by far the most abundant taxa. Finally, at Jago Chironomidae was abundant across most of the mudflat, but there were also small patches of abundant Oligochaeta, Amphipoda, and Tipulidae.

3.4.3 Shorebird Diet and Fattening Indices

We used isotopes to characterize and quantify shorebird diet and determine the marine component to the diet. Isotopic values of plasma $\delta^{13}C$ became significantly less depleted later in the season (early: $\delta^{13}C = -25.31 \pm 0.31$; late: $\delta^{13}C = -21.58 \pm 0.27$; F=0.644, df = 2 and 53, $P <$ 0.001) indicating a diet shift from terrestrial to marine food items at $\delta^{13}C \approx -24.00$ based on marine and tundra invertebrate samples (Churchwell et al. 2015). The mixing model isoscape (MixSIAR) suggests that the fractionation factor or diet breadth we modeled may not reflect the diet portrayed by the late-session plasma samples (Fig. 3.4), but we present the following mixing

model results letting the reader decide on the efficacy of this analysis method (also see Discussion). The mixing model found shorebirds feeding at Jago consumed Amphipoda and Oligochaeta; at Okpilak/Hulahula they consumed Chironomidae, Amphipoda, and Oligochaeta; and at Canning Spionidae, Oligochaeta, and Amphipoda (Fig. 3.5). In addition, the mixed model with random and fixed factors determined Jago and Okpilak/Hulahula shorebird abundance was associated with Amphipoda and Oligochaeta invertebrate abundance (similar to what we found in the mixing model analysis) and the feeding spatial scale was less than the delta spatial extent (Table 3.2) based on the significance of Easting.

We measured triglyceride levels and mass of migrants feeding at deltas (Canning N = 57, Okpilak/Hulahula N = 59, and Jago N = 64) as indicators of fattening rates as a proxy for habitat quality among sites (Fig. 3.6). Neither delta nor invertebrate abundance at the banding location explained differences in triglyceride levels; year, session, capture time, handling time, tarsus, and mass were significant explanatory variables (Table 3.3). In contrast, delta and invertebrate abundance at the capture locations were significant explanatory variables for bird mass as well as session and fat score (Table 3.4). In general, birds at Canning were heavier than the other two deltas late in the season (Fig. 3.6); on average two grams more than Okpilak/Hulahula and one gram more than Jago when comparing raw data values not adjusted for body size.

3.4.4 Avian Predation Pressure on Deltas

We found no difference in indices of predator use among deltas (F=0.653, df = 2 and 109, p = 0.523) or years (F=1.761, df = 1 and 109, p = 0.187), but there were more predators later in the season across all sites (F=8.864, df = 1 and 109, p = 0.004; Fig. 3.7). We ranked the deltas in terms of relative shorebird safety, and Canning was 100% free of predator cover because the study site is an island, Jago 76%, and Okpilak/Hulahula 61%.

3.5 Discussion

Our longest data set was four years of counts from Jago where we observed a peak of 3,000 to 4,000 Semipalmated Sandpipers each year (Fig. 3.3a), and this species used this delta consistently among years. The peak count was usually observed during just one count day. Although the magnitude of the peak was consistent, the timing of the peak fell anywhere within a 10-day period during the four survey years. This was likely the result of variability in the timing of the breeding season because of the large percentage of juvenile birds in the migrant population (S. Freeman personal communication). While the peak in shorebird use was observed early in the season at Jago, we observed low shorebird numbers early at Canning and Okpilak/Hulahula and a peak in use late during some years. In 2011, as counts declined at Jago, bird numbers at Okpilak/Hulahula increased to just over 4,000 birds, possibly in response to an increase in Oligochaeta abundance at that site. Our original hypothesis was the Jago and Okpilak/Hulahula would present similar bird numbers throughout the season because we thought the two deltas were close enough to each other to act as one unit spatially for the migrant population. The fact that these deltas are ≈ 20 km apart and had opposite trends in bird numbers suggests even naive juvenile birds are able to respond to small-scale changes in habitat quality while migrating. Interestingly, there was more similarity in shorebird phenology and abundance between the Canning and Okpilak/Hulahula deltas, which are 60 km apart, than the much closer Okpilak/Hulahula and Jago deltas.

Peak abundance of Semipalmated Sandpipers in early August corresponded with previous surveys (2005 and 2006) along the Beaufort Sea coast (Taylor et al. 2010). Semipalmated Sandpipers were present through the end of our surveys (24 August), but left the Beaufort Sea coast by 10 – 12 August in the previous study (Taylor et al. 2010). At the peak, we estimated >

500 Semipalmated Sandpipers/km^2 at the Jago; however, our average estimates were similar to densities previously recorded (Brown et al. 2012). Brown et al. (2012) estimated overall shorebird densities of 250 shorebirds/km^2 at Jago, 50 birds/km^2 at Okpilak/Hulahula, and 16 birds/km^2 at Canning averaging data from 2006 through 2010; 83% were Semipalmated Sandpipers. Our density estimates were higher for Okpilak/Hulahula and Canning, with ~250 Semipalmated Sandpipers/km^2 at peak migration. Differences in estimates of timing and abundance could be due to different survey methods. We counted birds every three days throughout migration and thus were probably better at capturing timing of the peak in migration and variation in shorebird numbers during the migration period, while previous studies focused one or two counts around the expected peak. Due to high cost and difficult access to count shorebirds in this region, the study design focusing on one or two counts during peak migration is common.

We found the majority of Semipalmated Sandpipers (98%) using these deltas were juveniles, which is similar to past estimates of 78-99% (Taylor et al. 2010, Brown et al. 2012). This suggests that Semipalmated Sandpipers have a juvenile-only migration pattern, where juveniles migrate on their own and sometimes use a different route than adults (Gill and Handel 1990). Additionally, variability in numbers and timing among years are likely reflective of productivity and phenology on the breeding grounds. For example, differences in the peak number of birds likely represent variable reproductive success; multiple peaks in migration may correlate with second nesting attempts. Second nesting attempts were found to be more common than previously thought in Dunlin (*Calidris alpina*; Gates et al. 2013), a similar species. The relationship between productivity and numbers of birds using coastal deltas confounds attempts to develop indices of habitat quality based on use. One solution is to collect several years of

invertebrate data to correlate with shorebird abundance, which provides insight into the annual variability in shorebird abundance and allows for inferences about habitat quality.

We also demonstrated that Semipalmated Sandpipers switched to an exclusively marine-derived diet once they arrived at the coastal mudflats. Post-breeding Semipalmated Sandpipers have been documented feeding on freshwater taxa (Baker 1977, Connors and Risebrough 1977), but it was unclear whether they foraged in both marine and adjacent upland tundra environments after reaching the coast. Isotopic analysis of blood plasma, which represents diet from the last 5-7 days for small shorebirds (Hobson and Clark 1993), showed a distinct shift between samples collected early and late in the post-breeding season. Blood plasma samples collected in the early period showed a mixed terrestrial and marine-derived diet, whereas later samples were all indicative of a marine-derived diet (δC^{13} = -20 to -24). Why birds transition to exclusively marine food resources is currently unknown, although several studies have found invertebrate abundance declines on the tundra after the breeding season (Tulp and Schekkerman 2008, Hill 2012). It is also possible shorebirds switch to foraging on delta invertebrates because they supply specific fatty acids that help fuel migration, such as the n-3 polyunsaturated fatty acids found in Amphipods (Pierce et al. 2011, Quinn and Hamilton 2012). Regardless of the reason, juvenile Semipalmated Sandpipers show a dependence on food resources at Beaufort Sea deltas during the first hop of migration.

Dependence on delta mudflats for foraging raises the question of differences in habitat quality among deltas, which we quantified using indices of blood triglycerides indicative of the food consumed during the previous half day (Williams et al. 1999) and body mass. We expected shorebird and invertebrate abundances, blood triglyceride levels, and shorebird body mass to all be similar and driven by high quality habitat. We found that invertebrate abundance did affect

the abundance of shorebirds. We found no differences, however, in blood triglyceride levels among deltas or capture locations within deltas. This discrepancy could be due to the efficiency of shorebird feeding, in that they are able to find sufficient food to increase triglyceride levels despite relatively low invertebrate abundance. In addition, we captured shorebirds in areas of high bird density within each delta. This may have biased our results because shorebirds congregated at sites with higher invertebrate abundance, which in turn could have led to high blood triglyceride levels. We have no evidence of a bias; however, the triglyceride values we observed were very similar to those observed in Western Sandpipers (*C. mauri*) (Guglielmo et al. 2002). In contrast to the triglycerides, we did find differences in shorebird body mass among deltas, although mass was not correlated with invertebrate abundance. The mean difference in body mass of birds among deltas was small (~1 g higher at the Canning than the other two deltas; unpublished data), thus it is unlikely to have biological relevance. Overall, we did not find any clear patterns in the indices of habitat quality we tested.

We often observed juvenile birds early in the post-breeding season with incomplete feather growth, thus juvenile Semipalmated Sandpipers were simultaneously finishing growth while fueling for and participating in migration. When individuals have increased energy demands because they are satisfying the requirements of multiple life-stages, it is referred to as a bottleneck period (Buehler and Piersma 2008), which are periods of increased vulnerability. For example, some populations of Red Knot (*C. canutus rogersi* and *C. c. rufa*) molt during their fall migration, and these bottlenecks have been correlated with their population declines (Buehler and Piersma 2008). Our research indicates juvenile Semipalmated Sandpipers may be growing and migrating simultaneously. While we do not have any indication that Semipalmated Sandpipers are negatively impacted during this period, the effects of a decline in juvenile

sandpipers may go unnoticed for many years due to the long-lived nature of shorebirds. Bottleneck periods would be good points in the life cycle to start investigating mechanisms of decline if Semipalmated Sandpipers from populations that are currently healthy start to decline. If the impact occurred in the juvenile population (on our study deltas for example) there would be a time lag, and it would be three or more years before the impact was observed in future counts of shorebirds on the deltas. For example, most juvenile Semipalmated Sandpipers do not return to the breeding grounds during their first year, and will not breed until the following year (Hicklin and Gratto-Trevor 2010).

Regardless of any strong indicators of habitat quality on the deltas based on fattening rates, isotopic analyses showed that sandpipers consumed different invertebrate taxa at each delta. The invertebrates consumed in the greatest proportion were Spionidae (Canning), Chironomidae (Okpilak/Hulahula) and Amphipoda (Jago), with Oligochaeta consumed in some proportion at all of the deltas. Isotopic signatures also indicated that shorebirds did not always consume the most common taxa found across a given delta, but concentrated feeding at a smaller scale on taxa that were locally abundant and patchily distributed. This concurs with other studies showing that shorebirds feed at small local scales (Alexander et al. 1996, Macdonald et al. 2012), but will change their diet depending on what is available (Skagen and Oman 1996, Davis and Smith 2001).

Shorebirds may select food items based on the amount of energy (in calories) that they provide. Caloric energy content of invertebrates changes through the season (Chironomidae 4900 – 6412 calories; Wissing and Hasler 1971) resulting in variability within a taxon. Because of variability in calories within taxa, estimates of caloric energy among taxa are relatively similar (4500 – 6412; Wissing and Hasler 1971, Gardner et al. 1985, Steimle and Terranova 1985). We

did not test invertebrates for energy content during the time that shorebirds were using the deltas, but in the future this information may help us understand why shorebirds are feeding on specific taxa. The literature suggests Amphipods have the lowest caloric energy content, yet the highest percentage of fat to body weight at 38%, which is almost twice that of the taxa with the next highest fat content (Chironomidae 23%; Gardner et al. 1985). Although some research suggests shorebirds may benefit from the consumption of specific fatty acids (Pierce et al. 2011) unexplored factors impacting the quantity and quality of consumed food items remain.

Although we did not have a species/taxon specific fractionation factor (Caut et al. 2009) for our isotopic data, we used a factor derived from captive Dunlin that were switched from a terrestrial to a marine diet (Ogden et al. 2004). However, some of the isotopic values from blood plasma fell outside the diet source polygon (a polygon created around the invertebrate samples displayed in Fig. 3.4), either indicating that the fractionation factor did not reflect reality or that one or more diet items consumed by the birds were not used in our analysis. However, plasma values that fell outside of the diet source polygon had higher $\delta^{15}N$ values than the food items, indicating that if we missed sampling a food item for analysis, it was higher on the trophic food chain. Recently, isotopic analysis of shorebird diet found that biofilm often accounts for a significant portion of shorebird diet (Quinn and Hamilton 2012, Kuwae et al. 2012). High $\delta^{15}N$ values found in our plasma samples indicate that neither biofilm (Quinn and Hamilton 2012) nor a lingering signature from terrestrial environments (Churchwell et al. 2015) accounts for the discrepancy between plasma and food items because both would have resulted in lower $\delta^{15}N$ signatures. One taxon we possibly missed sampling was the isopod Saduria, which we did not include because they were infrequently encountered in our invertebrate samples. This taxon is known to occupy two trophic levels depending on their size, and larger individuals have higher

$\delta^{15}N$ signatures (Churchwell et al. 2015); however, the size at which this taxon changes trophic level is unknown. However, most Saduria we observed were larger (> 6 cm) than what Semipalmated Sandpipers can consume. We suggest that the fractionation factor most likely accounted for the discrepancy in $\delta^{15}N$ between food items and plasma samples.

In addition to available food resources, use of stopover sites by shorebirds can also be influenced by the risk and perception of risk from predators (Pomeroy et al. 2006). We found that jaegers and Peregrine Falcons were the main predators of shorebirds using delta mudflats along the Beaufort Sea coast. Parasitic Jaegers were the most common predator, and some individuals seemed to specialize in catching shorebirds. In addition, the jaeger nestling stage lags slightly behind similar phenology of juvenile Semipalmated Sandpipers (Maher 1974). Although we found no difference in predator numbers among the three deltas, there were significantly fewer predators early in the migration period (often the peak in Semipalmated Sandpiper use of deltas) because many were still at upland breeding territories at this time. Despite the fact that numbers of predators did not vary among deltas, the perception of risk at each site was different. The Jago and Canning both included mudflats with little cover for predators to make an attack on shorebirds. Because the Canning is much smaller overall than the other deltas it may be difficult for migrating shorebirds to find and may have less use regardless of the quality of the habitat (Kraan et al. 2009b). The highest densities of Semipalmated Sandpipers were often found at the Jago early in the season even though it had similar invertebrate abundance to the other deltas, indicating shorebirds may prefer this site because of perceived safety from predation. In contrast, the Okpilak/Hulahula is a long narrow delta with abundant attack cover for predators, and typically supported very few shorebirds. Interactions between shorebirds and their predators are well documented (Ydenberg et al. 2002, Butler et al.

2003, Jamieson et al. 2014), and several authors suggest that shorebird predation may shape the timing of shorebird migration (Butler et al. 2003, Lank et al. 2011, Dekker et al. 2011). In general, we found fewer predators early in the season, and this may be one reason that the bulk of shorebird migration occurs during this period. We suggest shorebirds try to leave before Parasitic Jaegers and other predators have left their breeding territories on the uplands.

While the importance of staging areas that support large numbers of shorebirds like Delaware Bay and the Yellow Sea (Piersma 2007, Buehler and Piersma 2008, Yang et al. 2011) has become more evident, the role of short duration stopover sites in shorebird migration is less understood. For example, research at staging areas demonstrated that annual shorebird survival was linked to the success of migrant's ability to fatten during spring migration at Delaware Bay (Baker et al. 2004). However, our study population is a juvenile population that may use a different migration route as adults, thus, results demonstrating linkages between specific sites and demographics may be unattainable with our current technology for stopover sites like those found on the Beaufort Sea. On the other hand, if information on shorebird and invertebrate abundance for stopover and staging areas across the range of the three Semipalmated Sandpiper populations are collected, it may be possible to determine the importance of sites or at least migration corridors based on annual population trends. Focusing on whole life cycle questions for the three populations may help us determine causes of declines like those observed in the eastern population (Morrison et al. 1994, 2012). Our research provides insights into a portion of the larger picture. Whether it is the calories provided, a relatively predator free habitat, or fatty acids available in the abundant taxa, these deltas should be conserved because shorebirds are dependent on this marine habitat for the first hop of their migration.

3.6 Acknowledgements

We thank the many dedicated field technicians who helped collect samples. The National Fish and Wildlife Foundation, Bureau of Ocean Energy Management, US Fish and Wildlife Service Arctic National Wildlife Refuge, and the Arctic Landscape Conservation Cooperative funded this study. We had logistical support from the Arctic National Wildlife Refuge, USGS Alaska Cooperative Fish and Wildlife Research Unit, Institute of Arctic Biology, and Manomet Conservation Sciences. We had lab support from the Mark Wipfli aquatic invertebrate lab, Alaska Stable Isotope Facility, and the Alaska Sealife Center. We are also thankful to the Kaktovik Inupiat Corporation for letting us conduct research on their lands and the people of the village of Kaktovik for their help and friendship. We thank Dan Ruthrouff for his thoughtful review of this manuscript. Any use of trade product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the United States government. This research was conducted under IACUC approval # 148889.

3.7 References

Alerstam, T., and Å. Lindstrom. 1990. Optimal bird migration: the relative importance of time, energy, and safety. Pages 331–351 *in* E. Gwinner, editor. Bird Migration: The Physiology and Ecophysiology. Springer New York.

Alexander, S. A., A. Keith, C. L. Gratto-Trevor, and A. W. Diamond. 1996. Conventional and isotopic determinations of shorebird diets at an inland stopover: the importance of invertebrates and *Potamogeton pectinatus* tubers. Canadian Journal of Zoology 1068:1057–1068.

Baker, A. J., P. M. González, T. Piersma, L. J. Niles, I. de L. S. do Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proceeding of the Royal Society of London 271:875–882. doi: 10.1098/rspb.2003.2663.

Baker, M. C. 1977. Shorebird food habits in the eastern Canadian Arctic. Condor 79:56–62.

Beauchamp, G. 2009. Functional response of staging semipalmated sandpipers feeding on burrowing amphipods. Oecologia 161:651–655.

Beauchamp, G. 2010. Relationship between distance to cover, vigilance and group size in staging flocks of Semipalmated Sandpipers. Ethology:645–652. doi: 10.1111/j.1439-0310.2010.01778.x.

Beauchamp, G., M. Belisle, and L.-A. Giraldeau. 1997. Influence of conspecific attraction on the spatial Influence of learning foragers in a patchy habitat. Journal of Animal Ecology 66:671–682.

Beauchamp, G., and G. Ruxton. 2008. Disentangling risk dilution and collective detection in the antipredator vigilance of semipalmated sandpipers in flocks. Animal Behaviour 75:1837–1842. doi: 10.1016/j.anbehav.2007.12.016.

Brown, S., J. R. Bart, R. B. Lanctot, J. J. A. Johnson, S. Kendall, and D. Payer. 2007. Shorebird abundance and distribution on the coastal plain of the Arctic National Wildlife Refuge. Condor 109:1–14.

Brown, S., S. Kendall, R. Churchwell, A. Taylor, and A.-M. Benson. 2012. Relative shorebird densities at coastal sites in the Arctic National Wildlife Refuge. Waterbirds 35:546–554.

Buehler, D. M., and T. Piersma. 2008. Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 363:247–66. doi: 10.1098/rstb.2007.2138.

Butler, R. W., R. C. Ydenberg, and D. B. Lank. 2003. Wader migration on the changing predator landscape. Wader Study Group Bulletin 100:130–133.

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors (Δ 15 N and Δ 13 C): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46:443–453. doi: 10.1111/j.1365-2664.2009.01620.x.

Churchwell, R. T. C., S. J. Kendall, A. L. Blanchard, K. H. Dunton, A. N. Powell. 2015. Natural disturbance shapes benthic intertidal macroinvertebrate communities of high latitude river deltas. Estuaries and Coasts. *Online*. http://link.springer.com/10.1007/s12237-015-0028-2.

Connors, P. G., and R. W. Risebrough. 1977. Shorebird dependence on Arctic littoral habitats. Page Volume 3: 402–524 Environmental Assessment of the Alaskan Continental Shelf (Annual Reports of Principal Investigators). Outer-continental Shelf Environmental Assessment Program, Anchorage, Alaska.

Davis, C. A., and L. M. Smith. 2001. Foraging strategies and niche dynamics of coexisting shorebirds at stopover sites in the southern Great Plains. Auk 118:484–495.

Dekker, D., I. Dekker, D. Christie, and R. Ydenberg. 2011. Do staging Semipalmated Sandpipers spend the high-tide period in flight over the ocean to avoid falcon attacks along shore? Waterbirds 34:195–201. doi: 10.1675/063.034.0208.

Dunton, K. H., S. V. Schonberg, and L. W. Cooper. 2012. Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. Estuaries and Coasts 35:416–435.

Egevang, C., I. J. Stenhouse, R. A. Phillips, A. Petersen, J. W. Fox, and J. R. D. Silk. 2010. Tracking of Arctic Terns *Sterna paradisaea* reveals longest animal migration. Proceedings of the National Academy of Sciences of the United States of America 107:2078–81. doi: 10.1073/pnas.0909493107.

Gardner, W. S., T. F. Nalepa, W. A. Frez, E. A. Cichocki, and P. F. Landrum. 1985. Seasonal patterns in lipid content of Lake Michigan macroinvertebrates. Canadian Journal of Fisheries and Aquatic Sciences 42:1827–1832.

Gates, H. R., R. B. Lanctot, and A. N. Powell. 2013. High renesting rates in arctic-breeding Dunlin (*Calidris alpina*): a clutch-removal experiment. Auk 130:372–380. doi: 10.1525/auk.2013.12052.

Gill, R. E., and C. M. Handel. 1990. The importance of subarctic intertidal habitats to shorebirds: a study of the Central Yukon-Kuskokwim Delta, Alaska. Condor 92:709–725.

Gratto-Trevor, A. C., R. I. G. Morrison, D. Mizrahi, B. David, P. Hicklin, and A. L. Spaans. 2012a. Migratory connectivity of Semipalmated Sandpipers: winter distribution and migration routes of breeding populations. Waterbirds 35:83–95.

Gratto-Trevor, A. C., P. A. Smith, R. I. G. Morrison, and R. Cotter. 2012b. Population trends in Semipalmated Sandpipers from migration counts. Waterbirds 35:96–105.

Guglielmo, C. G., P. D. O'Hara, and T. D. Williams. 2002. Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free-living Western Sandpipers (*Calidris mauri*). Auk 119:437–445.

Harrington, B. A., and R. I. G. Morrison. 1979. Semiplamated Sandpiper migration in North America. Studies in Avian Biology 2:83–100.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4–18. doi: 10.1111/j.1365-2656.2010.01740.x.

Hicklin, P. W., and C. L. Gratto-Trevor. 2010. Semipalmated Sandpiper (*Calidris pusilla*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/species/006doi.10.2173/bna.6

Hicklin, P. W., and P. C. Smith. 1984. Selection of foraging sites and invertebrate prey by migrant Semipalmated Sandpipers, *Calidris pusilla* (Pallas), in Minas Basin, Bay of Fundy. Canadian Journal of Zoology 62:2201–2210.

Hill, B. L. 2012. Factors affecting survival of arctic-breeding Dunlin (*Calidris alpina arcticola*) adults and chicks. M.S. Thesis, University of Alaska Fairbanks. Fairbanks, Alaska.

Hobson, K. A., and R. G. Clark. 1993. Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. Auk 110:638–641.

Jamieson, S. E., R. C. Ydenberg, and D. B. Lank. 2014. Does predation danger on southward migration curtail parental investment by female western sandpipers? Animal Migration 2:34–43. doi: 10.2478/ami-2014-0004.

Johnson, J. A., R. B. Lanctot, B. A. Andres, J. R. Bart, S. Brown, S. Kendall, and D. Payer. 2007. Distribution of breeding shorebirds on the Arctic Coastal Plain of Alaska. Arctic 60:277–293.

Kraan, C., J. A. van Gils, B. Spaans, A. Dekinga, A. I. Bijleveld, M. van Roomen, R. Kleefstra, and T. Piersma. 2009a. Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. Journal of Animal Ecology 78:1259–1268.

Kraan, C., J. van der Meer, A. Dekinga, and T. Piersma. 2009b. Patchiness of macrobenthic invertebrates in homogenized intertidal habitats: hidden spatial structure at a landscape scale. Marine Ecology Progress Series. 383:211-224.

Kuwae, T., E. Miyoshi, S. Hosokawa, K. Ichimi, J. Hosoya, T. Amano, T. Moriya, M. Kondoh, R. C. Ydenberg, and R. W. Elner. 2012. Variable and complex food web structures revealed by exploring missing trophic links between birds and biofilm. Ecology Letters. 15:347–356. doi: 10.1111/j.1461-0248.2012.01744.x.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Chris-Tensen. 2013. Package lmerTest. http://cran.r-project.org/web/packages/lmerTest/lmerTest.pdf.

Lank, D. B., R. W. Butler, J. Ireland, and R. C. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. Oikos 103:303–319.

Lank, D. B., R. W. Butler, J. Ireland, R. C. Ydenberg, and R. C. Effects. 2011. Effects of predation danger on migration strategies of sandpipers. Oikos 103:303–319.

Lindstrom, Å., M. Klaassen, T. Piersma, N. Holmgren, and L. Wennerberg. 2002. Fuel stoes of juvenile waders on autumn migration in high arctic Canada. Ardea 90:93–101.

Macdonald, E. C., M. G. Ginn, and D. J. Hamilton. 2012. Variability in foraging behavior and implications for diet breadth among Semipalmated Sandpipers staging in the Upper Bay of Fundy. Condor 114:135–144. doi: 10.1525/cond.2012.100246.

Maher, W. J. 1974. Ecology of Pomarine, Parasitic, and Long-Tailed jaegers in northern Alaska. Pacific Coast Avifauna 88:157. doi: 137.224.18.34.

Maillet, D., and J. M. Weber. 2006. Performance-enhancing role of dietary fatty acids in a long-distance migrant shorebird: the Semipalmated Sandpiper. Journal of Experimental Biology 209:2686–95. doi: 10.1242/jeb.02299.

Marsh, P., and T. Schmidty. 1993. Influence of a Beaufort Sea storm surge on channel levels in the Mackenzie Delta. Arctic 46:35–41.

Martin, P. D. 1983. Bird use of arctic tundra habitats at Canning River Delta, Alaska. M.S. Thesis. University of Alaska, Fairbanks, Fairbanks, Alaska.

McWilliams, S. R., S. B. Kearney, and W. H. Karasov. 2002. Diet preferences of warblers for specific fatty acids in relation to nutrional requirements and digestive capabilities. Journal of Avian Biology 33:167–174.

Morrison, R. I. G., C. Downes, and B. Collins. 1994. Population trends of shorebirds on fall migration in eastern Canada 1974-1991. The Wilson Bulletin 106:431–447.

Morrison, R. I. G., D. S. Mizrahi, R. K. Ross, H. Otte, N. De Pracontal, and A. Narine. 2012. Dramatic declines of Semipalmated Sandpipers on their major wintering areas in the Guianas, northern South America. Waterbirds 35:120–134.

NOAA. 2010. NOAA Tide Predictions: Flaxman Island 2010. Retrieved from http://tidesandcurrents.noaa.gov/get_predictions.shtml?year=2010&stn=7292+Kodiak&secstn=Flaxman+Island&thh=0&thm=57&tlh=0&tlm=28&hh*0.08&hl=*0.09&footnote.

Norton, D., and G. Weller. 1984. The Beaufort Sea: background, history, and perspective. Pages 3–22 *in* P. W. Barnes, D. M. Schell, and E. Reimnitz, editors. The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press, Inc., Orlando.

Ogden, L. J. E., K. A. Hobson, and D. B. Lank. 2004. Blood isotopic ($\delta^{13}C$ and $\delta^{15}N$) turnover and diet-tissue fractionation factors in captive Dunlin (*Calidris alpina pacifica*). Auk 121:170–177.

Pierce, B. J., S. R. McWilliams, T. P. O'Connor, A. R. Place, and C. G. Guglielmo. 2005. Effect of dietary fatty acid composition on depot fat and exercise performance in a migrating songbird, the Red-eyed Vireo. Journal of Experimental Biology 208:1277–85. doi: 10.1242/jeb.01493.

Pierce, B. J., S. R. McWilliams, and S. Url. 2011. Seasonal changes in composition of lipid stores in migratory birds : causes and consequences. Condor 107:269–279.

Piersma, T. 1987. Hop, skip, or jump? Constraints on migration of arctic waders by feeding, fattening, and flight speed. Limosa 60:184–185.

Piersma, T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. Journal of Ornithology 148:45–59. doi: 10.1007/s10336-007-0240-3.

Pomeroy, A. C. 2005. Tradeoffs between food abundance and predation danger in spatial usage of a stopover site by Western Sandpipers, *Calidris mauri*. Oikos 3:1-9.

Pomeroy, A. C., R. W. Butler, and R. C. Ydenberg. 2006. Experimental evidence that migrants adjust usage at a stopover site to trade off food and danger. Behavioral Ecology 17:1041–1045. doi: 10.1093/beheco/arl043.

Pomeroy, A. C. 2006. Tradeoffs between food abundance and predation danger in spatial usage of a stopover site by Western Sandpipers, *Calidris mauri*. Oikos 3:629–637.

Porter, R., and P. A. Smith. 2013. Techniques to improve the accuracy of location estimation using light-level geolocation to track shorebirds. Wader Study Group Bulletin 120:147–158.

Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montaña. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–89. doi:10.1007/s00442-006-0630x.

Quinn, J. T., and D. J. Hamilton. 2012. Variation in diet of Semipalmated Sandpipers (*Calidris pusilla*) during stopover in the upper Bay of Fundy, Canada. Canadian Journal of Zoology 1190:1181–1190. doi: 10.1139/Z2012-086.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Semmens, B., and E. Ward. 2014. MixSIAR. Retrieved from http://conserver.iugo-cafe.org/user/brice.semmens/MixSIAR.

Skagen, S. K., and F. L. Knopf. 1994. Residency patterns of migrating sandpipers at a midcontinental stopover. Condor 96:949–958.

Skagen, S. K., and H. D. Oman. 1996. Dietary flexibility of shorebirds in the western hemisphere. Canadian Field Naturalist 110:419–444.

Smith, P. A., C. L. Gratto-trevor, B. T. Collins, D. Fellows, R. B. Lanctot, J. Liebezeit, B. J. Mccaffery, J. Rausch, S. Kendall, S. Zack, and H. R. Gates. 2012. Trends in abundance of Semipalmated Sandpipers: evidence from the Arctic. Waterbirds 35:106–119.

Steimle, F. W., and R. J. Terranova. 1985. Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. Journal of Northwest Atlantic Fisheries Science 6:117–124.

Taylor, A. R., R. B. Lanctot, A. N. Powell, S. J. Kendall, and D. A. Nigro. 2011. Residence time and movements of postbreeding shorebirds on the northern coast of Alaska. Condor 113:779–794. doi: 10.1525/cond.2011.100083.

Taylor, A. R., A. N. Powell, D. A. Nigro, and S. J. Kendall. 2010. Distribution and community characteristics of staging shorebirds on the northern coast of Alaska. Arctic 63:451–467.

Tulp, I., and H. Schekkerman. 2008. Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. Arctic 61:48–60.

Warnock, N. 2010. Stopping vs. staging: the difference between a hop and a jump. Journal of Avian Biology 41:621–626. doi: 10.1111/j.1600-048X.2010.05155.x.

Williams, T. D., C. G. Guglielmo, O. Egeler, and C. J. Martyniuk. 1999. Plasma lipid metabolites provide information on mass change over several days in captive Western Sandpipers. Auk 116:994–1000.

Wissing, T. E., and A. D. Hasler. 1971. Intraseasonal change in caloric content of some freshwater invertebrates. Ecology 52:371–373.

Yang, H. Y., B. Chen, M. Barter, T. Piersma, C. F. Zhou, F. S. Li, and Z. W. Zhang. 2011. Impacts of tidal land reclamation in Bohai Bay, China: ongoing losses of critical Yellow Sea waterbird staging and wintering sites. Bird Conservation International 21:241–259. doi: 10.1017/S0959270911000086.

Ydenberg, R. C., R. W. Butler, D. B. Lank, C. G. Guglielmo, M. Lemon, and N. Wolf. 2002. Trade-offs, condition dependence and stopover site selection by migrating sandpipers. Journal of Avian Biology 33:47–55.

Table 3.1. Invertebrate abundance (mean ± S.E.; range) at three delta mudflats along the eastern Beaufort Sea, Alaska, 2010 – 2011. Two taxa, Chironomidae and Oligochaeta, are not presented because they are shown in Fig. 3.3. Superscript [F] = freshwater taxa, [M] = marine taxa, [B] = commonly found in both marine and freshwater environments, and [T] = terrestrial taxa. ** taxa not found.

	2010			2011		
	Canning	Okpilak/Hulahula	Jago	Canning	Okpilak/Hulahula	Jago
Amphipoda[M]	112.8 ± 38.5	3.3 ± 2.5	20.1 ± 10.2	73 ± 39.8	9.6 ± 5.1	29.2 ± 12.5
	(0 - 3000)	(0 - 600)	(0 - 2000)	(0-4500)	(0 - 1300)	(0 - 2600)
Arachnida[T]	**	**	**	**	**	0.4 ± 0.4
	**	**	**	**	**	(0 - 100)
Capniidae[T]	**	0.4 ± 0.4	**	**	**	0.8 ± 0.6
	**	(0 - 100)	**	**	**	(0 - 100)
Chaetiliidae[M]	4 ± 1.8	4.1 ± 1.4	1.2 ± 0.7	**	1.4 ± 0.9	1.2 ± 0.7
	(0 - 100)	(0 - 200)	(0 - 100)	**	(0 - 200)	(0 - 100)
Collembola[F]	**	**	**	1.6 ± 1.2	1.8 ± 1.1	0.8 ± 0.6
	**	**	**	(0 - 100)	(0 - 200)	(0 - 100)
Copopoda[F]	**	**	**	**	1.4 ± 1.1	0.4 ± 0.4
	**	**	**	**	(0-300)	(0 - 100)
Cicadellidae[T]	**	**	0.4 ± 0.4	**	**	**
	**	**	(0 - 100)	**	**	**
Culicidae[F]	**	0.4 ± 0.4	2.0 ± 0.9	0.8 ± 0.8	**	0.4 ± 0.4
	**	(0 - 100)	(0 - 100)	(0-100)	**	(0 - 100)
Empididae[F]	**	**	**	**	0.4 ± 0.4	**
	**	**	**	**	(0 - 100)	**
Ephydridae[F]	**	**	**	0.8 ± 0.8	**	0.4 ± 0.4
	**	**	**	(0-100)	**	(0 - 100)
Hydrachnidia[F]	**	**	**	**	0.4 ± 0.4	**
	**	**	**	**	(0 - 100)	**
Hymenoptera[T]	**	**	**	**	0.7 ± 0.5	**
	**	**	**	**	(0 - 100)	**
Nematode[B]	**	**	**	1.6 ± 1.6	51.8 ± 17.7	12.0 ± 4.5

Table 3.1 Continued

	**	**
Plecoptera[F]	**	**
	**	**
Spionidae[M]	24 ± 10.9	**
	(0 - 1000)	**
Tipulidae[F]	**	11.9 ± 3.2
	**	(0 - 500)

**	(0 - 200)	(0 - 3100)	(0 - 900)
**	**	0.7 ± 0.7	**
**	**	(0 - 200)	**
**	14.6 ± 17.3	3.2 ± 2.5	**
**	(0 - 800)	(0 - 700)	**
47.1 ± 8.6	0.8 ± 0.8	24.5 ± 10.3	53.1 ± 12.1
(0 - 1100)	(0-100)	(0 - 2500)	(0 - 1900)

Table 3.2. The relationship between shorebird and invertebrate abundance found at three delta mudlfats along the eastern Beaufort Sea, Alaska, 2010-2011. The significant mixed (REML) model variables are presented for Jago and Okpilak/Hulahula River deltas.

Random Variables						Fixed Variables				
Variable	Variance	SD	χ^2	DF	p	Variable	Estimate	SE	t	p
Session	2.639	1.624	44.6	1	<0.000	Intercept	-1596	595.7	-2.679	0.007
Year	0.952	0.976	12.5	1	<0.000	Easting	0.000	0.000	2.683	0.007
Residual	142.980	11.957				Amphipoda	0.005	0.002	2.233	0.026
						Oligochaeta	0.000	0.000	2.776	0.006

Table 3.3. Sources of variation in triglyceride levels of Semipalmated Sandpiper blood collected at three delta mudflats along the eastern Beaufort Sea coast, Alaska, 2010-2011. Significant variables ($\alpha \leq 0.05$) are presented in the ANCOVA model of birds we captured at the Jago, Okpilak/Hulahula, and Canning River deltas.

Variable	Estimate	S.E.	t value	p
Intercept	1.11	0.51	2.19	0.030
Year	0.23	0.06	3.74	0.000
Session	0.40	0.07	5.85	0.000
Capture Time	0.00	0.00	3.46	0.001
Handling Time	-0.02	0.01	-3.35	0.001
Tarsus	-0.07	0.02	-3.17	0.002
Weight	0.04	0.01	3.71	0.000

Table 3.4. Sources of variation in mass of Semipalmated Sandpipers captured at three delta mudflats along the eastern Beaufort Sea, Alaska, 2010-2011. Significant variables ($\alpha \leq 0.05$) in the ANCOVA model of birds we banded at the Jago, Okpilak/Hulahula, and Canning River deltas.

Variable	Estimate	S.E.	t value	p
Intercept	0.999	0.018	54.462	0.000
Session	0.083	0.020	4.221	0.000
Fat	0.038	0.008	4.865	0.000
Delta (Jago)	-0.045	0.021	-2.159	0.032
Delta (Okpilak)	-0.076	0.024	-3.179	0.002
Invert. Abund.	-0.001	0.000	-2.013	0.046

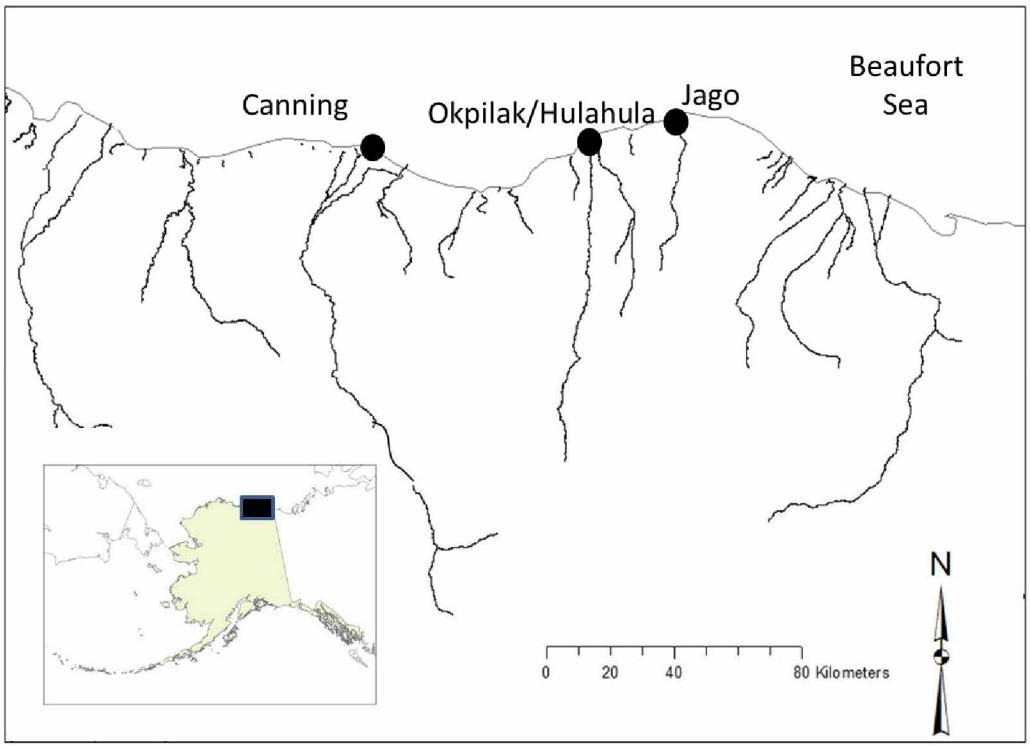

Figure 3.1. Locations of three study sites where invertebrate and shorebird data were collected along the eastern Beaufort Sea, Alaska, 2009 – 2012.

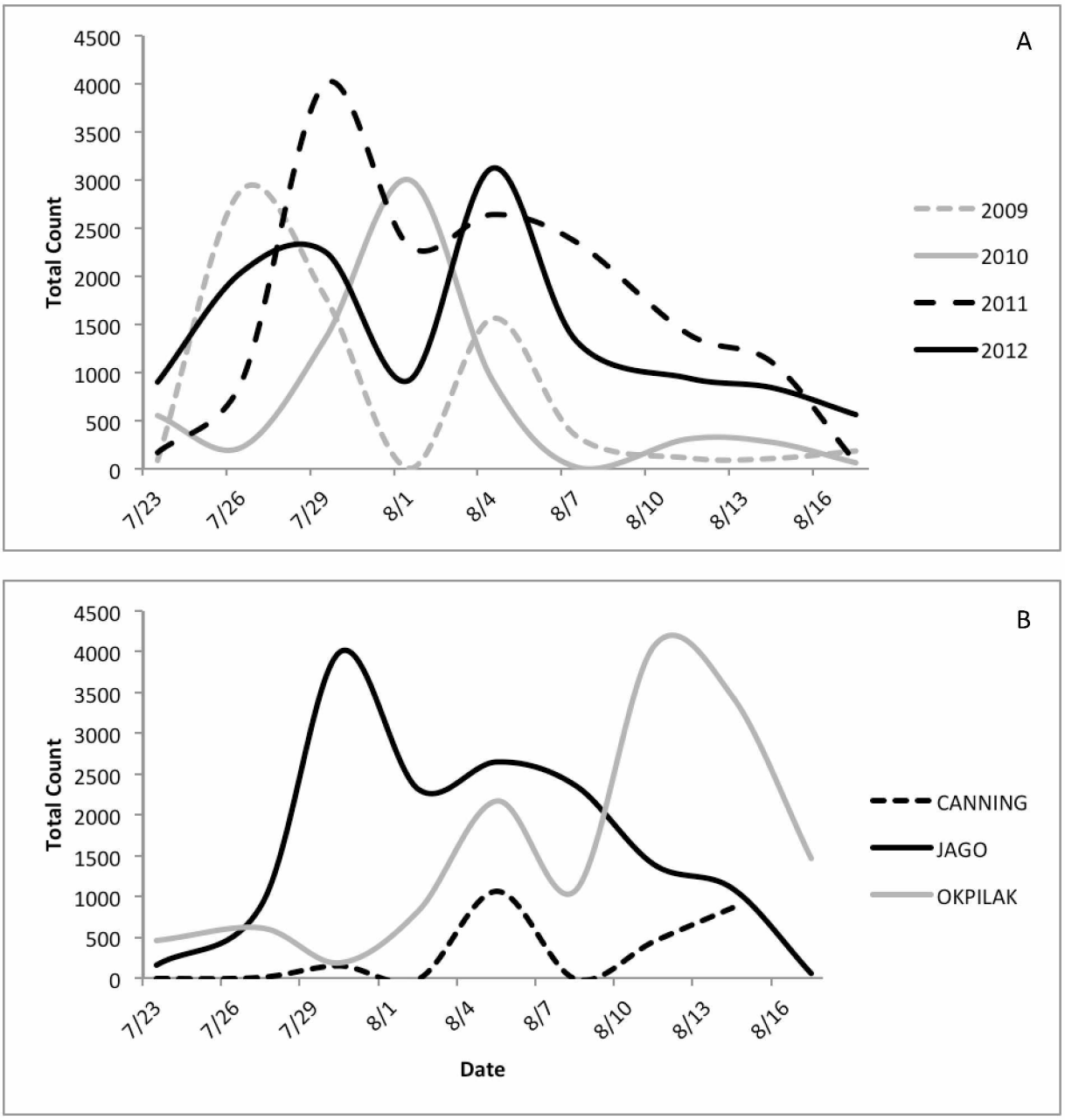

Figure 3.2. Total counts of Semipalmated Sandpipers at (A) Jago 2009 – 2012, and (B) all three deltas (Jago, Okpilak/Hulahula, and Canning) 2011. Counts were conducted every three days.

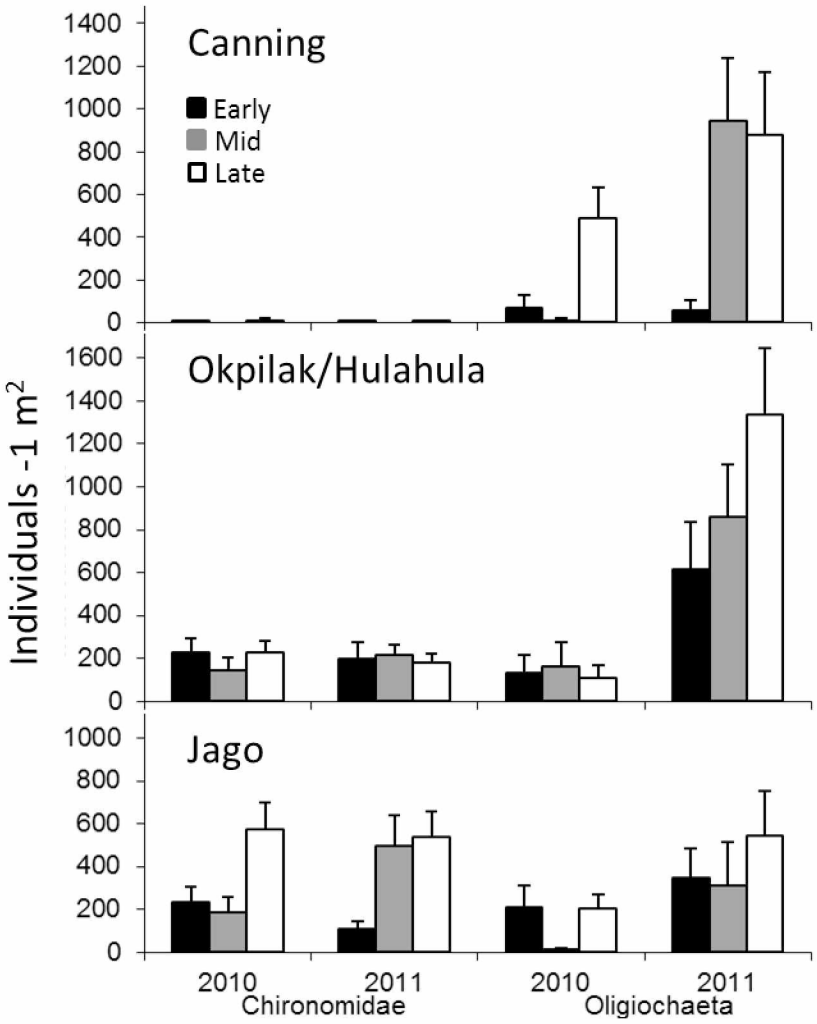

Figure 3.3. Abundance (mean ± S.E.) of Chironomidae and Oligochaeta at three river deltas along the eastern Beaufort Sea coast, Alaska, 2010 – 2011. The black, grey, and white bars represent the early, mid, and late sampling sessions.

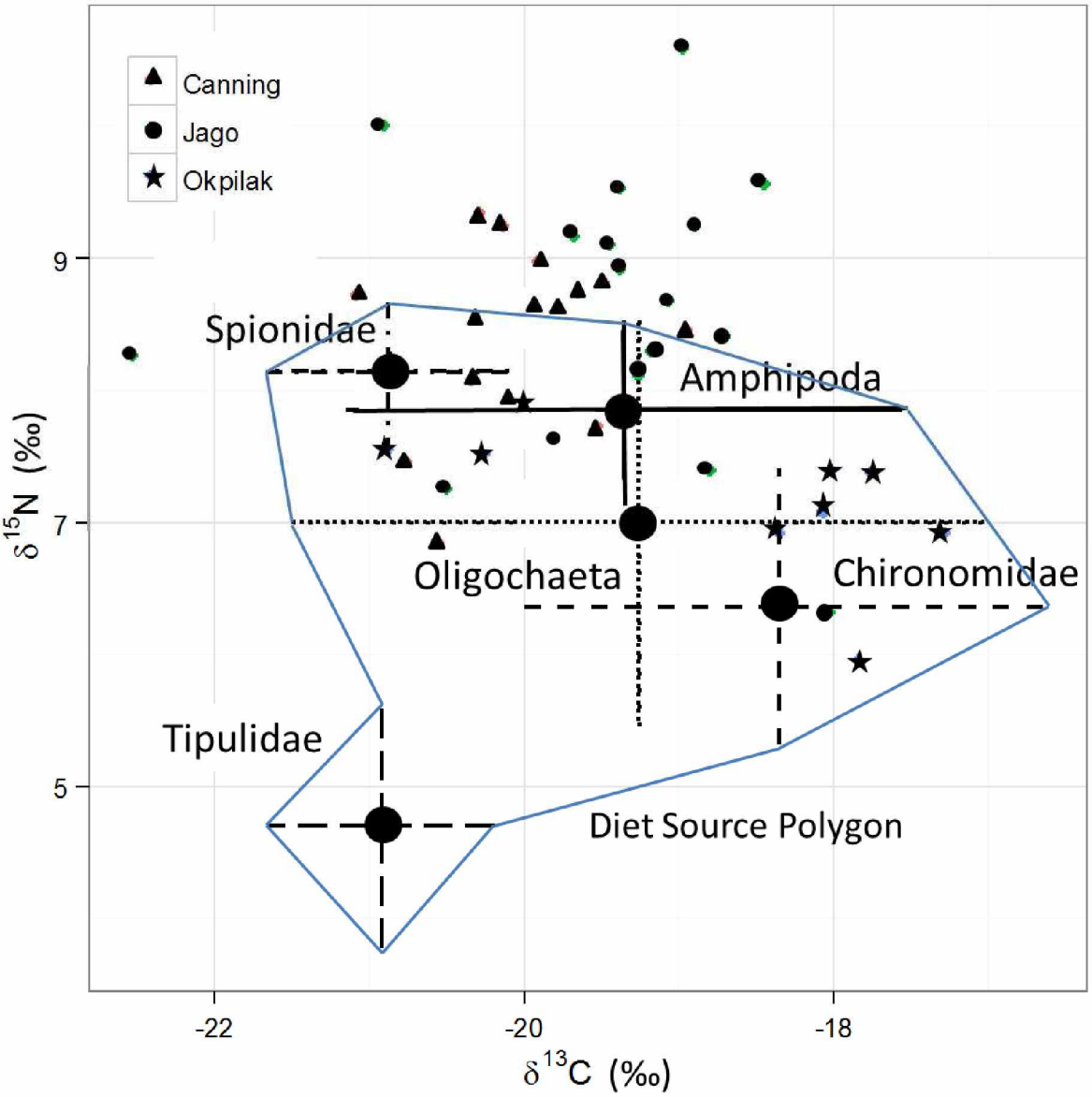

Figure 3.4. Isoscape of $\delta^{13}C$ and $\delta^{15}N$ derived in a Bayesian MixSIAR model from blood plasma (symbols) from hatch-year Semipalmated Sandpiper and invertebrate food items (means ± S.E.) at three river deltas along the eastern Beaufort Sea, Alaska, 2010 – 2012.

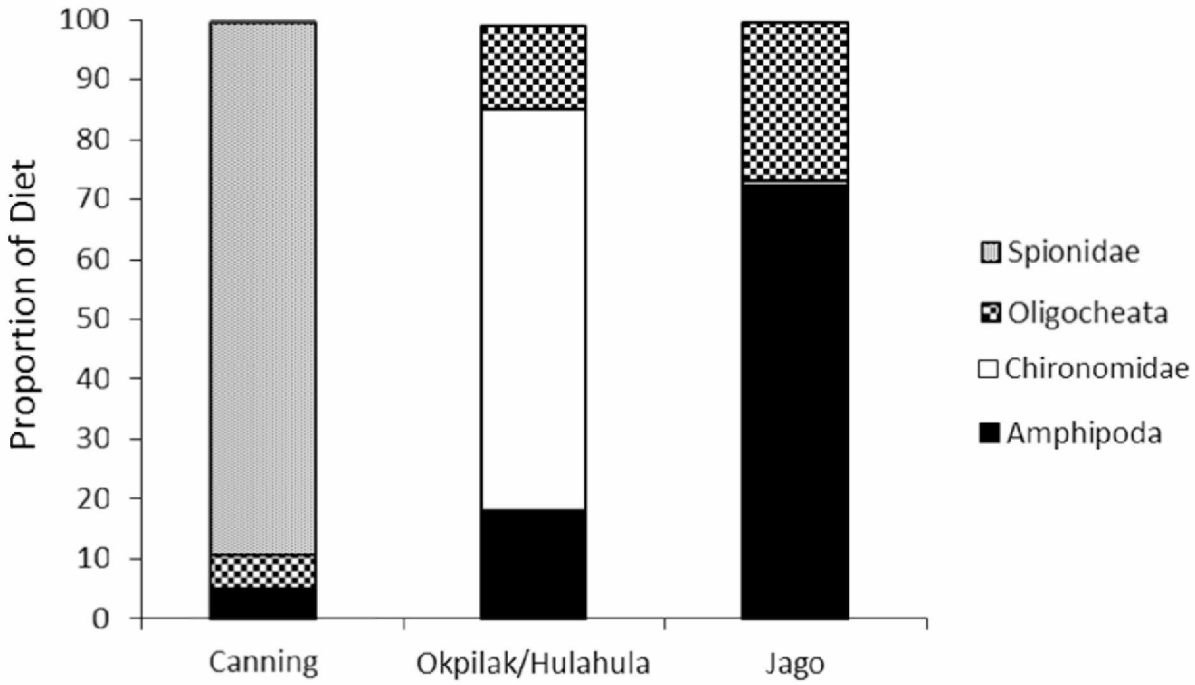

Figure 3.5. Proportion of commonly occurring invertebrate taxa in the diet of hatch-year Semipalmated Sandpipers at three river deltas along the eastern Beaufort Sea, Alaska. Values were derived using a Bayesian mixing model (MixSIAR) from shorebird blood plasma and invertebrates collected during the late season migration period.

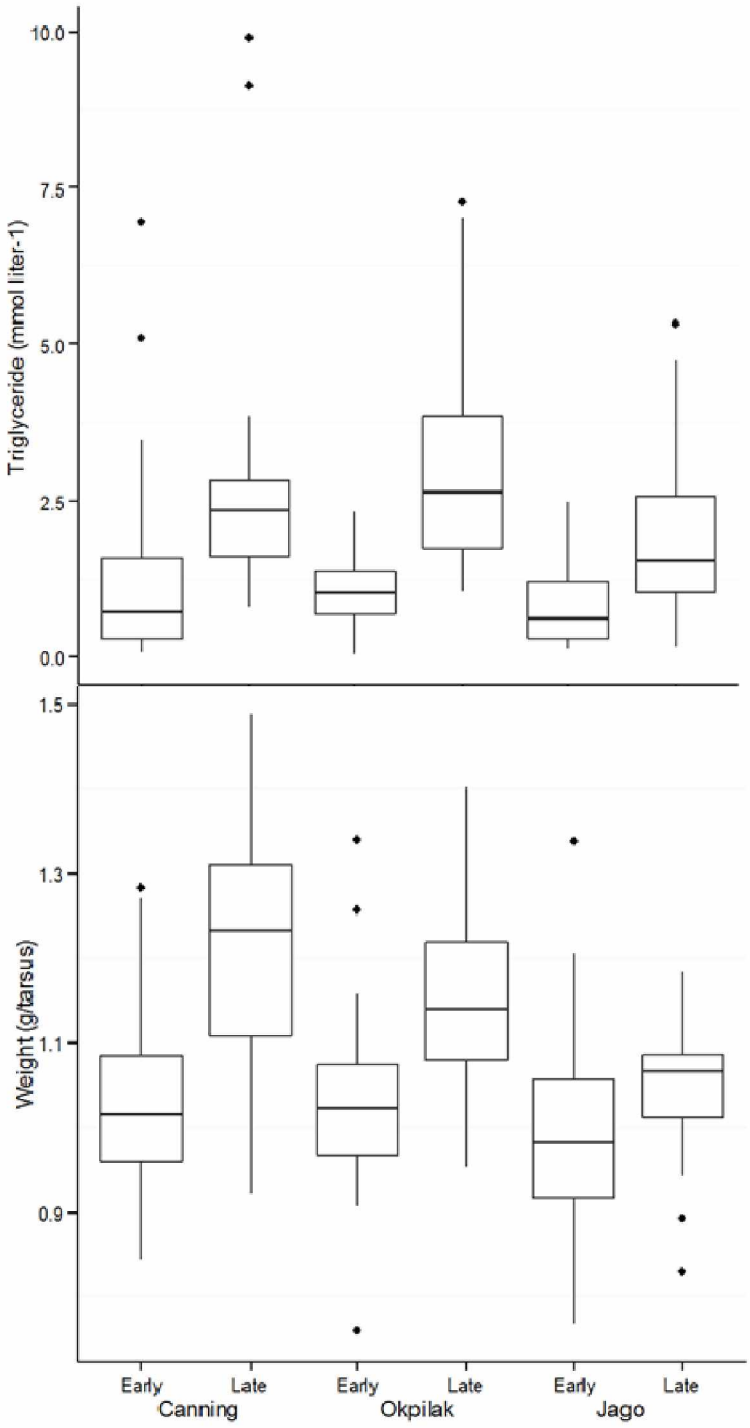

Figure 3.6. Triglyceride levels and mass of hatch-year Semipalmated Sandpipers during early and late season migration periods, at three river deltas along the eastern Beaufort Sea, Alaska 2010 – 2011. Box plot boundaries are standard errors.

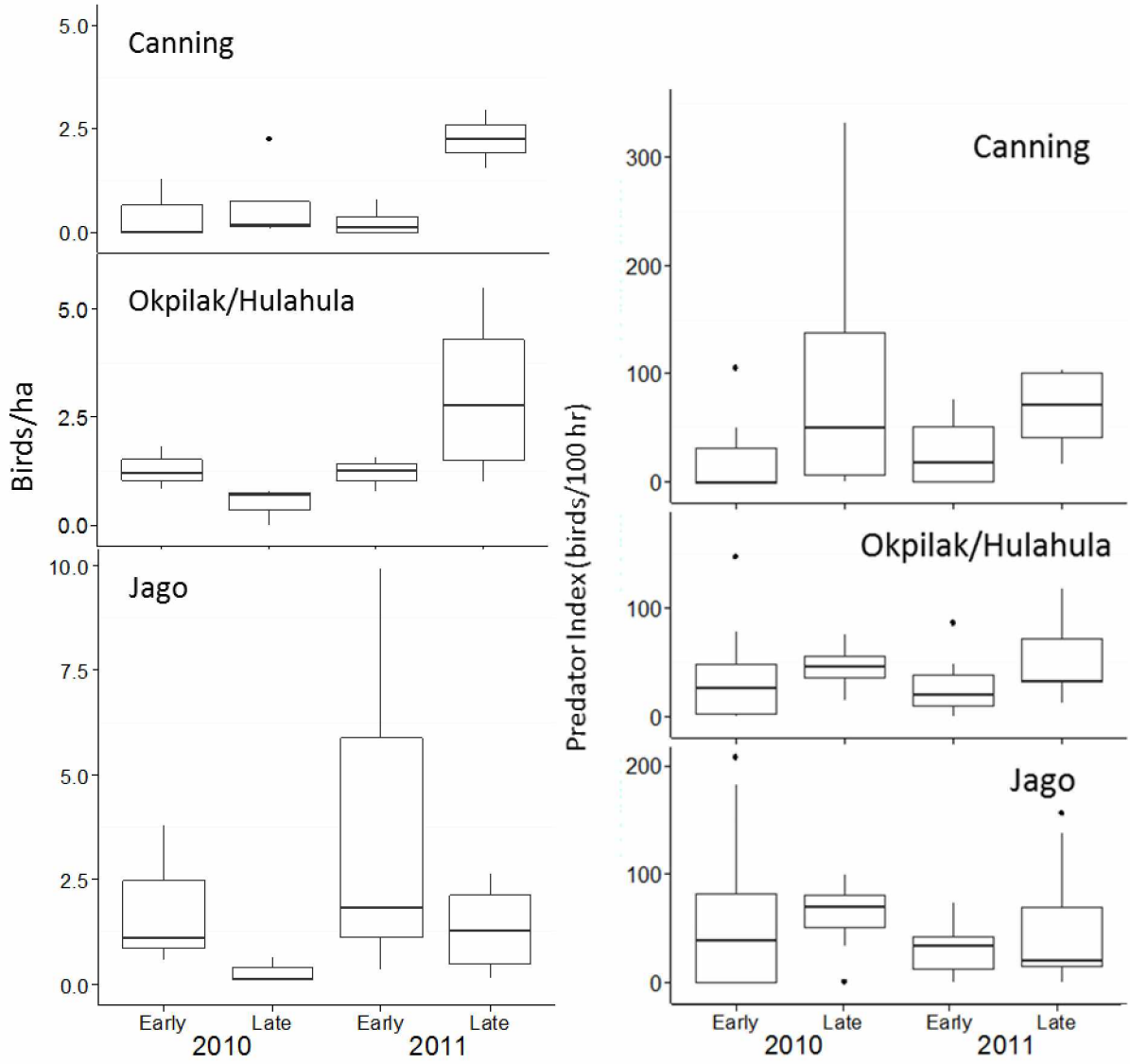

Figure 3.7. Abundances of Semipalmated Sandpipers and indices of avian predators for three river deltas along the eastern Beaufort Sea, Alaska, 2010 – 2011. Shorebird abundance and the predator index are presented by banding session for comparison with triglyceride and weight values.

4 Storm Surge and Tidal Impacts on Food Availability for Semipalmated Sandpipers at the Beginning of Fall Migration[1]

4.1 Abstract.

Tens of thousands of shorebirds use Beaufort Sea river deltas to start their fall migration. Especially prevalent are hatch-year Semipalmated Sandpipers (*Calidris pusilla*) that make up 83% of all shorebird detections. Our research was focused on foraging habitat; we mapped out available foraging habitat at water levels we observed during shorebird counts conducted in early (21 July – 1 August), mid (1 – 8 August), and late (10 – 22 August) survey sessions in the migration period. We compared the calories available for birds to forage on at these observed water levels with modeled values derived from water level changes due to lunar tides and then again from changes due to storm surges. The calories available to foraging shorebirds were significantly greater for observed water levels versus lunar tide water levels and significantly greater for lunar tide water levels versus storm surge water levels. We also observed that the largest peak in shorebird migration occurred at the end of the early session at the Jago, but later peaks occurred at the Okpilak/Hulahula and Canning deltas. Furthermore, the peak in forage availability occurred during the late session, which is mismatched with the largest peak in migration during the early session at the Jago delta. Future warming may allow shorebirds to migrate earlier, but because forage availability is affected more by water levels than invertebrate emergence times, there may be an even greater mismatch between peak migration and food availability. Furthermore, future changes in climate will likely increase storm surges that

[1] To be submitted to Waterbirds: Churchwell, R.T., S. Kendall, S.C. Brown, A.N. Powell. (XXXX) Storm surge and tidal impacts on food availability for Semipalmated Sandpipers at the beginning of fall migration.

negatively impact shorebird migration due to increased storm frequency and declines in sea ice, which are the major factors causing storm surge.

4.2 Intoduction

Stored fats are the main source of nutrients and fuel for avian migration (Ramenofsky 1990, Jenni and Jenni-Eiermann 1998, Landys et al. 2005), and it is assumed the fat deposition at stopover sites is a critical component of a successful migration (McWilliams and Karasov 2001, Krapu et al. 2006, Maillet and Weber 2006, Hua et al. 2013). Stopover sites are crucial in the successful migration of many birds, but particularly for arctic-breeding shorebirds that migrate long distances from breeding to wintering grounds (Galbraith et al. 2002, Skagen 2006, Iwamura et al. 2013). Food resources needed for each migration bout are tied to a species' migration strategy; long-distance migrants need more resources to refuel at a stopover site than short-distance migrants (Choi et al. 2009). Shorebirds that make short-distance migrations of hundreds of kilometers and stops of a day or two use a "hop" migration strategy, long distance migrations are "jump" strategies where birds travel nonstop for thousands of kilometers and stop over for extended periods of weeks to fuel at stopover sites, and "skip" migration strategies have migration distances and stopover times between a hop and a jump (Piersma 1987, Warnock 2010). Some shorebird populations rely on specific stopover locations with the majority of the population refueling at these sites (Iwamura et al. 2013). Because large portions of a population can depend on specific locations, these sites are considered migration bottlenecks, and impacts to these sites can quickly affect the shorebird population (Buehler and Piersma 2008, Iwamura et al. 2013). Despite the importance of stopover sites, a direct link between sufficient food resources at stopover sites overall and migration success has been difficult to establish. However, a negative correlation between food intake at a critical stopover site at Delaware Bay and annual

survival of Red Knots (*Calidris canutus*) suggested that subsequent migration to their arctic breeding grounds was unsuccessful for those birds with lower body weights (Baker et al. 2004).

The Arctic Coastal Plain of Alaska supports breeding populations of long and short-distance migrant shorebirds, and > 200,000 shorebirds are estimated to breed within the coastal plain of the Arctic National Wildlife Refuge (Brown et al. 2007). After breeding, many of these shorebirds begin their fall migration at the Beaufort Sea, where they feed at coastal river deltas, presumably to fatten for their next flight (Taylor et al. 2010, Brown et al. 2012). The majority of these shorebirds (83%; Brown et al. 2012) are hatch-year (recently fledged) Semipalmated Sandpipers (*C. pusilla*) preparing for their first migration. During this portion of their migration these sandpipers are using a "hop" migration strategy, staying at a river delta for a day or so and then traveling ~100 km to the next stop (Taylor et al. 2011). The importance of these deltas as stopover sites has not been established, but the presence of tens of thousands of shorebirds foraging at these sites at the onset of fall migration suggests they supply fuel for the first leg of migration.

The mudflats on which these shorebirds are foraging along the Beaufort Sea coast are associated with lagoons protected from the open marine environment by barrier islands. There are three major river deltas within the Arctic National Wildlife Refuge where we conducted our research: the Okpilak/Hulahula and Jago rivers are glacial-fed rivers, while the Canning River is strictly spring fed. These differences influence the substrates in which invertebrates (shorebird prey) are found; glacially influenced rivers and their associated deltas have finer sediments and a flush of fresh water from the melting glaciers during the peak of summer (Nolan et al. 2011). Differences in freshwater influence and sediment type result in patchily distributed invertebrates, in terms of both abundance and type, on the mudflats used by foraging shorebirds (Churchwell et

al. 2015). This can lead to a patchy distribution of shorebirds on deltas as well; we found a positive correlation between abundance of invertebrates and Semipalmated Sandpipers at shorebird foraging habitat (Churchwell Chapter 2).

In general, foraging habitat for shorebirds at these river deltas is reliably available because of the minimal tidal influence along the Beaufort Sea coast. Unlike most other coastal areas, the lunar high tide is not great enough to inundate shorebird feeding areas. The maximum diurnal lunar tide effect results in water level change of only 30 cm, and averages 10.5 cm (NOAA 2010). However, storm surge events can completely inundate delta mudflats at random intervals (Crane 1974, Moitoret 1983, Marsh and Schmidty 1993, Pisaric et al. 2011, Vermaire et al. 2013). On the Beaufort Sea, the surge effect is the product of an interaction between the Beaufort Gyre that flows from east to west along Alaska's north coast, and atmospheric pressure, wind speed, and wind direction (Norton and Weller 1984). Storm winds from the west create an increasing storm surge, while strong winds from the east cause water levels to drop (Crane 1974, Norton and Weller 1984). The effect winds have on surge height may be tempered early in the season if sea ice is still present because the ice dampens the wave action (Reimnitz and Maurer 1979); however, future climate change scenarios predict increased incidences of storm surges in arctic seas because of an expected decline in sea ice (Overeem et al. 2011, Rampal et al. 2011, Massonnet et al. 2012) and increased storm frequency (Walsh 2008, Overeem et al. 2011). These storm surges occur throughout the fall shorebird migration, which happens during the ice-free period of mid-July through mid-September. The impacts of increased frequency of storm surges on forage availability for migrating shorebirds at the onset of fall migration are of concern.

We examined relationships between timing of fall migration and storm surges with respect to forage availability for Semipalmated Sandpipers on the Beaufort Sea coast by using different water level scenarios to predict impacts on food availability for fueling migration. First, we determined the phenology of fall migration for hatch-year Semipalmated Sandpipers at the three major river deltas within the Arctic National Wildlife Refuge. We then estimated calories available to foraging shorebirds derived from systematic sampling of invertebrates at the three river deltas. Next, we determined changes in calories available to shorebirds based on several different water level scenarios, including seasonal variation, lunar tides, and storm surges. These analyses will lead to a better understanding of the importance of these stopover sites to migrant shorebirds as well as the potential impacts of increased frequency of storm surges in the Beaufort Sea due to climate change.

4.3 Methods

4.3.1 Study Area

As part of a large-scale study on the ecology of shorebirds during the first stage of their fall migration, we sampled invertebrates at three river deltas (Canning, Okpilak/Hulahula, and Jago) on the coast of the Arctic National Wildlife Refuge in northeastern Alaska (Fig. 4.1). The Jago delta is the farthest east and approximately 650 ha, the Okpilak/Hulahula is 20 km to the west (740 ha), while the smallest site, Canning, is another 60 km west (290 ha). The mudflats where shorebirds feed consist of sand, silt, and clay sediments; no gravels were observed (Churchwell et al. 2015). While it is typical for coastal deltas to have regular inputs of seawater the Jago and Okpilak/Hulahula mudflats were characterized by freshwater (zero salinity), except for small areas on their western ends due to constant river flows and low tides. In contrast, about

25-50% of Canning River delta's perimeter was saline (12-20‰), depending on the prevailing ocean currents (Churchwell unpublished data).

4.3.2 Shorebird Phenology

Shorebird counts were conducted at each delta between the third week in July as the nesting season finished, and the third week in August, when most of the Semipalmated Sandpipers had moved south, 2010 and 2011. We first established a 100 x 100 m grid system delineated by wooden lathes on each delta, and the species, number, and age of birds were recorded within each cell. The grid scale used to survey shorebirds was smaller than was used for invertebrate collection (described below) because it was not possible to visually quantify shorebirds within the larger grid. At each delta, we surveyed shorebirds every three days counting birds across entire deltas each survey-day. Even though we had 24-hr daylight for much of the survey period, we counted birds starting in the mid-morning (around 0900) until we covered the survey area, which took 6-8 hrs on the larger deltas. We did not count birds later in the evening because shorebird activity declined (Andres 1989).

We present total daily counts for Semipalmated Sandpipers to represent an estimate of the number of birds on each delta on a given survey day. We did not account for detection probability because detection rates for shorebirds in this habitat were previously estimated to be 0.99 (Brown et al. 2012).

4.3.3 Invertebrate Sampling

To determine spatial and temporal patterns of invertebrate abundance, we used a stratified random sampling framework, with a grid of 250- x 250-m cells, which covered all available shorebird feeding habitat at each of the three deltas. Invertebrates were sampled from a random location within each grid cell. We only sampled areas with water depths ≤ 5 cm,

because that was determined to be accessible to feeding shorebirds based on bill length. If water depth at a sample location was > 5 cm it was not sampled during that session; a second random location within each grid square was evaluated for water depth and sampled instead. If both locations were > 5 cm then the grid cell was not considered foraging habitat. We collected an invertebrate core and when water was present, recorded water depth to the nearest cm at each sample location. We used a PVC corer (1/100 m^2) pushed into the sediment to 5-cm depth (volume = 501.2 cm^3) to sample invertebrates. We sifted the core through a 500-µm sieve and stored preserved invertebrates and residual sediment in a plastic jar with 70% alcohol. To capture temporal patterns of invertebrate abundance and distribution, we collected samples at each delta during three time periods (sessions) corresponding with fall migration: early (21 July – 1 August), mid- (1 – 8 August) and late (10 – 22 August) 2010 and 2011.

In the lab, we sorted invertebrate samples by taxa to the family level when possible. We identified samples to a higher taxonomic level than family when individuals were difficult to identify and were rare, or the taxonomic level met the ecological level of interest as a shorebird food item. We counted individuals in the invertebrate core and extrapolated this to biomass using published length-weight regressions specific to each taxon. The taxa-specific biomass measurements were then converted to calories m^{-2} by multiplying by 5400 cal·g^{-1} invertebrate dry weight (Table 4.1). The calories per gram of dry weight is an estimate based on an average for Chironomidae, Ologochaeta, Amphipoda, and Polychaeta (Wissing and Hasler 1971, Wacasey and Atkinson 1976, Steimle and Terranova 1985), which is very similar to a commonly used estimate for all invertebrates of 5500 cal·g^{-1} invertebrate dry weight (Van de Kam et al. 2004). All of the taxa in our study were soft-bodied invertebrates and easily digested, thus we did not consider digestibility in our analysis. The calorie estimates for each sample location and

session were then used as the basis for our analysis of available feeding habitat and potential fuel for migration.

4.3.4 Water Levels

Because water level equates to the amount of available feeding habitat for shorebirds on a mudflat, we calculated habitat boundaries for each delta using water levels observed during shorebird counts. We mapped water levels every three days by outlining the water's edge as we conducted each shorebird count: approximately three water level maps were produced for each sampling session. We then averaged these water level maps to create a map to represent average water levels for the early-, mid-, and late-season sessions. We assumed that by averaging three maps per session we accounted for lunar tides and storm surges that may have influenced our water-level measurements and thus provide the best baseline estimates. These water level maps became the baseline boundaries used in our analyses to represent the foraging habitat available to shorebirds without lunar tide or surge effects.

The second group of maps represented tidal influences added to our average water level maps. To incorporate additional water level height due to lunar tides, we created new mudflat boundaries using GIS. These boundaries accounted for the additional horizontal distance in water inundation calculated from the average slope of our deltas resulting from a 10.5 cm (the average lunar tide; NOAA 2010) increase in water level. Because it was not possible to survey all three deltas for slope due to logistical constraints, we used a slope of 0.000741 $m \cdot m^{-1}$ based on previous measurements from the Jago Delta. When we considered slope in addition to increased water level from an average lunar tide, there was a change of about 140 m of horizontal distance (habitat lost under water) across each mudflat. Finally, we created another group of maps estimating the amount of foraging habitat available during a storm surge using

water depths measured with a barometric pressure data logger deployed in each lagoon during the study. We defined a surge as changes in water level greater than a maximum lunar tide (> 30 cm). We calculated surge water levels by subtracting 30 cm from actual barometric pressure data logger water measurements, and any positive values were due to a surge. Because we wanted to compare the surge values to our average tide values, we added these positive values to an average lunar tide (+ 10.5 cm) for analysis. These calculations resulted in yearly measurements of surge effect values of about 208 m and 321 m horizontal distance across each mudflat in 2010 and 2011 respectively.

We also had surge level data in 2009 from the barometric pressure data logger, but had no invertebrate biomass data from that year for comparison. However, we included data from 2009 in a graphic of surge water levels to demonstrate the annual and seasonal variability in surge effect.

4.3.5 Analyses

We used a kriging method to determine the distribution of calories from invertebrates using the R library geoR (Ribeiro and Diggle 2013). Kriging is a geostatistical technique that uses the spatial variance between pairs of sample points to model the predicted values from each sample location, which is then extrapolated across the study area (Fig. 4.2; Fortin and Dale 2005). In the kriging analysis, we created a variogram using an exponential model, fit the model, and projected the model as a predictive map for each delta. These kriging maps of calories m^{-2} were created to evaluate differences in potential forage availability for each year, delta, session, and water level combination. From each map, we calculated total calories available across each delta, which was the sum of values of the 250 x 250 m predictive raster grid cells output in each kriging script. We compared the different combinations using percent change, and conducted

paired t-tests to test for a significant difference between the observed, tidal, and surge estimates. We were unable to create maps for the Canning delta in early and mid-sessions for 2010 and early-session in 2011 because there were too few invertebrates on the delta for the kriging models to converge on an estimate.

4.4 Results

We present data from 2009 through 2012 for the Jago delta to describe phenological use of the sites by foraging shorebirds, but only present data for 2011 for the other deltas to describe variation among study sites (Fig. 4.3) because patterns were similar among years. The number of Semipalmated Sandpipers using the Jago delta peaked in the early session, on average around 1 August (range = 26 July – 5 August; Fig. 4.3A). Peak counts at the Jago delta were 3,000 to 4,000 birds, and the peak occurred for just one count day before numbers declined by 1,500 birds. Peak counts at the other two deltas were not observed during the early session; at the Okpilak/Hulahula a peak of 4,000 birds was counted on 12 August (Fig. 4.3B).

The amount of foraging habitat, expressed as total calories m^{-2}, varied among the three sites, with the most calories available at the Jago delta (160,376 total calories averaged across sessions), and the least overall at the Okpilak/Hulahula delta (95,523 total calories; Fig. 4.4). Patterns of seasonal variability also differed by site. At the Okpilak/Hulahula delta, available foraging habitat did not vary much among sessions. In contrast, the Canning and Jago deltas had more available foraging habitat in the late sessions than the two earlier sessions (Fig. 4.4). We found Chironomidae contributed just as many calories as Oligochaeta in 2010, but this taxon was not found at the Canning Delta (Table 4.1). In 2011, the majority of calories came from Oligochaeta, and this taxon was commonly found at all deltas. During both years marine

invertebrates contributed more calories at the Canning Delta than at the other two deltas (Table 4.1).

The estimated effect of the lunar tide produced available caloric estimates that averaged 66% (range 36-81%) of the available calories calculated for observed baseline water levels. In paired t-tests from combined sites, calories available during lunar tides were significantly lower than the baseline values ($t = 6.9$, $df = 14$, $P < 0.001$). The estimated effect of surge tides on available calories was 42% (range 0-75%) of baseline water levels, and the amount of calories available during surge tides was significantly lower than calories during lunar tides ($t = 3.6$, $df = 14$, $P = 0.003$). Of our modeled tides, a surge tide occurring mid-season at the Canning delta was the only one that would have completely inundated the entire mudflat, resulting in no foraging habitat available for shorebirds. In fact, actual observations at the Canning indicated there was complete inundation of the delta during two days for about a four-hour period due to the combination of a storm surge plus a lunar tide hitting its cycle maximum.

Actual surge tides were relatively common and unpredictable from 2009 – 2011 (Fig. 4.5). However, they were less frequent during the early session. Many storm surges were one-day events and occurred for 24 hours or less, but there were multiday events on 8 - 11 August 2009 and 15 - 17 August 2010. There was only one surge event that resulted in water levels > 1 m at all three deltas in 2009, which completely inundated the deltas and all mudflat foraging habitat (Churchwell personal observation). All other surge events resulted in water levels less than a maximum lunar tide (< 30 cm).

4.5 Discussion

We found variation in foraging habitat (available calories) among deltas and sessions within the migration period. The greatest amount of foraging habitat occurred during the late

session. This was likely due to low water in lagoons because the lowest river discharges occur during this period (USGS 2012), corresponding with minimal snow and glacier melt in the Brooks Range due to cooling temperatures (Churchwell personal observation). We also found the Jago Delta had the highest forage available. Our 2010 estimates were more similar to the other deltas, but 2011 estimates demonstrated that there can be annual variation. These differences suggest that there may be opportunities for shorebirds to time migration to the peak in forage during some years. We also observed variation in the timing of peak shorebird migration among the three sites, and one possibility is that migrants may take advantage of differing forage availability with the greatest peak in migration early at the Jago Delta early in the season, while the peak was later at the other deltas.

We found Semipalmated Sandpiper stopover use of Beaufort Sea delta mudflats mostly occurred around the first few weeks of August. The timing of fall migration is partially dependent on spring snowmelt and the initiation of nesting (Newton 2008) that occurs in mid-June. Then the sandpipers move to the coast after fledging in mid-July to start their west to east migration along the Beaufort Sea coast (Taylor et al. 2011). Climate warming has the potential to impact the timing of nesting by shifting nest initiation earlier in the breeding season (Grabowski et al. 2013, Liebezeit et al. 2014), and earlier nest initiation would lead to earlier departure from the breeding grounds by adults and juveniles. Earlier departure dates would correspond to current periods of low storm surge frequency (Overeem et al. 2011), potentially maximizing the amount of foraging habitat available on Beaufort Sea delta mudflats. Currently the peak in migration occurs about the time that storm surges become more common. Another consideration is the phenology of invertebrate prey available on the mudflats may preclude any advantage of earlier arrival of shorebirds at these sites; we found that the greatest invertebrate

abundance, biomass, and available calories for fattening were found at the end of the migratory season (Fig. 4.4; Churchwell et al. 2015). However, none of these processes are static, and climate warming predictions also suggest that storm surges (Overeem et al. 2011) and invertebrate emergence could occur earlier in the future similar to changes suggested for upland areas (Liebezeit et al. 2014).

We were not able to tie the amount of available habitat to whether these juvenile shorebirds migrate successfully, but several factors point to the importance of this habitat as stopover sites for hatch-year Semipalmated Sandpipers. First, based on observed undeveloped feather tracks, short wing chords, and low weights, some juvenile birds were still growing when they began their migration (Churchwell unpublished data). In addition, the majority of adult birds seem to leave the breeding grounds by a different route based on the few adults observed in our study and others (Taylor et al. 2010, Brown et al. 2012). In another species, the Sharp-tailed Sandpiper (*C. acuminata*), where juvenile birds used a different migration route than adults, it was suggested juveniles might need more food resources than adults to complete a successful migration (Handel and Gill 2010). Juveniles migrating on the Beaufort Sea coast don't have competition from adults, and it is possible the coastal migration route provides more feeding opportunities than the route used by the majority of adult birds, which allows for securing more resources for continued growth and migration preparation. Second, juvenile Semipalmated Sandpipers may be showing an adaptation to variable resources by using a "hop" migration strategy along the Beaufort Sea coast since short flights with many feeding stops (Warnock 2010) would allow for adjustments to changing conditions and food availability. Finally, Beaufort Sea deltas could be considered a "bottleneck" for the juvenile age class (Buehler and Piersma 2008) because of the large number of Alaskan juvenile Semipalmated Sandpipers that

use the areas to fuel their southern migration. Bottleneck stopover sites have been shown to be critical to population survival for several shorebird migrants (Piersma 2002, Buehler and Piersma 2008), and impacts to these deltas may cause a decline in the Alaskan Semipalmated Sandpiper population if juvenile migration is unsuccessful, leading to lower survival of this age class.

In contrast to Alaskan-breeding sandpipers, shorebirds migrating at more southern latitudes time their daily feeding around a diurnal tidal schedule. However, for shorebirds feeding on the Beaufort Sea coast foraging habitat is available all hours of the day because of minimal lunar tides. Regardless, our models demonstrated that even relatively low lunar tides could potentially reduce the number of calories available to foraging shorebirds by up to 80% during high tides. Even though foraging habitat was available, at another Beaufort Sea delta there was an observed decrease in foraging by shorebirds in the middle of the day and during the night hours (Andres 1989). It has been suggested that shorebirds rest during the night hours because cooler temperatures during the evening influence thermodynamics for the birds and the availability of invertebrates as forage (Andres 1989, Van de Kam et al. 2004). Unfortunately, we did not document the timing of resting periods to know whether they coincided with lunar high tides.

During our study, we observed highly variable and unpredictable storm surges (Fig. 4.5), including a storm surge that completely inundated the Canning delta for only a few hours on two days. However, we observed complete inundation events that lasted $\geq$ 24 hours while conducting other research in 2008 and 2009. In the future, climate change impacts are expected to increase the frequency and severity of such storm events. Decreasing coverage by sea ice (Overeem et al. 2011, Perovick et al. 2014) allows for increased severity in storm surge because ice can dampen wave action (Reimnitz and Maurer 1979, Overeem et al. 2011). It is also

expected that the frequency in storms will increase in the Beaufort Sea during the open-water period (Atkinson 2005, Walsh 2008, Hinzman et al. 2013). In addition to impacts on availability of overall shorebird feeding habitat, storm surges can also directly affect the composition of the invertebrate community (Pisaric et al. 2011, Vermaire et al. 2013). Benthic invertebrates have specific salinity and sediment requirements (Yates et al. 1993, Kraan et al. 2010), and storm surges can increase the salinity of deltas via seawater inundation, and change the particle size of sediments (Vermaire et al. 2013) by washing away fine sediments. Some important food resources, such as Chironomidae inhabit sediments with fine particle size and low salinity (Churchwell et al. 2015); increased storm surges could negatively impact their abundance and distribution within delta mudflats.

To our knowledge this work is the first to investigate tidal change and storm surge impacts on foraging habitat at stopover sites. Previous research on the effects of storm surges have focused on impacts to nesting birds (Fienup-Riordan 1999, Van de Pol et al. 2010, Craik et al. 2015), and the impacts of sea-level rise at shorebird stopover sites (Galbraith et al. 2002, Austin and Rehfisch 2003, Iwamura et al. 2013).

We suggest that future research should incorporate available forage into a functional response model of shorebird feeding rates at different invertebrate densities. We planned to use a model similar to the one developed for Red Knots feeding on bivalves at different densities (Piersma et al. 1995, Van Gils et al. 2004, Kraan et al. 2009), but we found that a similar model did not exist in the literature for small shorebirds feeding on soft-bodied prey. Development of such a model was beyond the scope of this project, but development of such a model would improve an analysis such as ours.

4.6 Acknowledgements

We thank the many dedicated field technicians who helped collect samples. The National Fish and Wildlife Foundation, Bureau of Ocean Energy Management, US Fish and Wildlife Service Arctic National Wildlife Refuge, and the Arctic Landscape Conservation Cooperative funded this study. We had logistical support from the Arctic National Wildlife Refuge, USGS Alaska Cooperative Fish and Wildlife Research Unit, Institute of Arctic Biology, and Manomet Conservation Sciences. We had lab support from the Mark Wipfli aquatic invertebrate lab. We are also thankful to the Kaktovik Inupiat Corporation for letting us conduct research on their lands and the people of the village of Kaktovik for their help and friendship. Any use of trade product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the United States government. This research was conducted under IACUC approval # 148889.

4.7 References

Andres, B. A. 1989. Littoral zone use by post-breeding shorebirds on the Colville River Delta, Alaska. M.S. Thesis. Ohio State University, Columbus, Ohio.

Atkinson, D. E. 2005. Observed storminess patterns and trends in the circum-arctic coastal regime. Geo-Marine Letters 25:98–109. doi: 10.1007/s00367-004-0191-0.

Austin, G. E., and M. M. Rehfisch. 2003. The likely impact of sea level rise on wader (Charadrii) wintering on estuaries. Journal for Nature Conservation 11:43–58.

Baker, A. J., P. M. González, T. Piersma, L. J. Niles, I. L. S. Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in Red Knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proceeding of the Royal Society of London 271:875–882. doi: 10.1098/rspb.2003.2663.

Brown, S., J. R. Bart, R. B. Lanctot, J. A. Johnson, S. Kendall, D. Payer, and J. Johnson. 2007. Shorebird abundance and distribution on the coastal plain of the Arctic National Wildlife Refuge. Condor 109:1–14.

Brown, S., S. Kendall, R. Churchwell, A. Taylor, and A.-M. Benson. 2012. Relative shorebird densities at coastal sites in the Arctic National Wildlife Refuge. Waterbirds 35:546–554.

Buehler, D. M., and T. Piersma. 2008. Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 363:247–66. doi: 10.1098/rstb.2007.2138.

Choi, C., X. Gan, Q. Ma, K. Zhang, J. Chen, and Z. Ma. 2009. Body condition and fuel deposition patterns of calidrid sandpipers during migratory stopover. Ardea 97:61–70.

Churchwell, R. T., S. J. Kendall, A. L. Blanchard, K. H. Dunton, and A. N. Powell. 2015. Natural disturbance shapes benthic intertidal macroinvertebrate communities of high latitude river deltas. Estuaries and Coasts. doi: 10.1007/s12237-015-0028-2.

Craik, S. R., A. R. Hanson, R. D. Titman, and L. Matthew. 2015. Potential impacts of storm surges and sea-level rise on nesting habitat of Red-breasted Mergansers (*Mergus serrator*) on barrier islands in New Brunswick , Canada. Waterbirds 38:77–85.

Crane, J. J. 1974. Ecological studies of the benthic fauna in an arctic estuary. M.S. Thesis. University of Alaska, Fairbanks, Fairbanks, Alaska.

Fienup-Riordan, A. 1999. Yaqulget qaillun pilartat (What the birds do): Yup'ik Eskimo understanding of geese and those who study them. Arctic 52:1–22.

Fortin, M.-J., and M. Dale. 2005. Spatial Analysis. Cambridge University Press, Cambridge.

Galbraith, A. H., R. Jones, R. Park, J. Clough, and G. Page. 2002. Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. Waterbirds 25:173–183.

Grabowski, M. M., F. I. Doyle, D. G. Reid, D. Mossop, and D. Talarico. 2013. Do arctic-nesting birds respond to earlier snowmelt? A multi-species study in north Yukon, Canada. Polar Biology 36:1097–1105. doi: 10.1007/s00300-013-1332-6.

Handel, C. M., and R. E. Gill. 2010. Wayward youth: trans-Beringian movement and differential southward migration by juvenile Sharp-tailed Sandpipers. Arctic 63:273–288.

Hinzman, L. D., C. J. Deal, A. D. McGuire, S. H. Mernild, I. V Polyakov, and J. E. Walsh. 2013. Trajectory of the Arctic as an integrated system. Ecological Applications 23:1837–68. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/24555312.

Hua, N., T. Piersma, and Z. Ma. 2013. Three-phase fuel deposition in a long-distance migrant, the Red Knot (*Calidris canutus piersmai*), before the flight to high arctic breeding grounds. PLoS ONE 8:1–6. doi: 10.1371/journal.pone.0062551.

Iwamura, T., H. P. Possingham, I. Chadès, C. Minton, N. J. Murray, I. Danny, E. A. Treml, and R. A. Fuller. 2013. Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. Proceeding of the Royal Society of London:20130325. Retrieved from http://dx.doi.org/10.1098/rspb.2013.0325.

Jenni, L., and S. Jenni-Eiermann. 1998. Fuel supply and metabolic constraints in migrating birds. Journal of Avian Biology 29:521–528.

Kraan, C., G. Aarts, J. van der Meer, and T. Piersma. 2010. The role of environmental variables in structuring landscape-scale species distributions in seafloor habitats. Ecology 91:1583–1590.

Kraan, C., J. A. van Gils, B. Spaans, A. Dekinga, A. I. Bijleveld, M. van Roomen, R. Kleefstra, and T. Piersma. 2009. Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. Journal of Animal Ecology 78:1259–1268.

Krapu, G. L., J. L. Eldridge, C. L. Gratto-Trevor, and D. A. Buhl. 2006. Fat dynamics of arctic-nesting sandpipers during spring in mid-continental North America. Auk 123:323–334.

Landys, M. M., T. Piersma, C. G. Guglielmo, J. Jukema, M. Ramenofsky, J. C. Wingfield, and M. M. Landys-Ciannelli. 2005. Metabolic profile of long–distance migratory flight and stopover in a shorebird. Proceedings of the Royal Society B: Biological Sciences 272:295–302. doi: 10.1098/rspb.2004.2952.

Liebezeit, J. R., K. E. B. Gurney, M. Budde, S. Zack, and D. Ward. 2014. Phenological advancement in arctic bird species: relative importance of snow melt and ecological factors. Polar Biology. doi: 10.1007/s00300-014-1522-x.

Maillet, D., and J. M. Weber. 2006. Performance-enhancing role of dietary fatty acids in a long-distance migrant shorebird: the Semipalmated Sandpiper. Journal of Experimental Biology 209:2686–95. doi: 10.1242/jeb.02299.

Marsh, P., and T. Schmidty. 1993. Influence of a Beaufort Sea storm surge on channel levels in the Mackenzie Delta. Arctic 46:35–41.

Massonnet, F., T. Fichefet, H. Goosse, C. M. Bitz, G. Philippon-Berthier, M. M. Holland, and P. Y. Barriat. 2012. Constraining projections of summer arctic sea ice. Cryosphere 6:1383–1394. doi: 10.5194/tc-6-1383-2012.

McWilliams, S. R., and W. H. Karasov. 2001. Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology 128:579–93. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11246046.

Moitoret, C. S. 1983. Bird use of arctic coastal shorelines at Canning River Delta, Alaska. M.S. Thesis. University of Alaska Fairbanks. Fairbanks, Alaska.

Newton, I. 2008. The Migration Ecology of Birds. Elsevier LTD, London.

NOAA. 2010. NOAA Tide Predictions: Flaxman Island 2010. Retrieved from http://tidesandcurrents.noaa.gov/get_predictions.shtml?year=2010&stn=7292+Kodiak&secstn=Flaxman+Island&thh=-0&thm=57&tlh=-0&tlm=28&hh=*0.08&hl=*0.09&footnote=.

Nolan, M., R. Churchwell, J. Adams, J. McClelland, K. D. Tape, S. Kendall, A. Powell, K. Dunton, D. Payer, and P. Martin. 2011. Predicting the impact of glacier loss on fish, birds, floodplains, and estuaries in the Arctic National Wildlife Refuge. Pages 49–54 *in* C. N. Medley, G. Patterson, and M. J. Parker, editors. Observing, Studying, and Managing for Change. US Geological Survey Scientific Investigations Report 2011- 5169, Reston, Virginia.

Norton, D., and G. Weller. 1984. The Beaufort Sea: background, history, and perspective. Pages 3–22 *in* P. W. Barnes, D. M. Schell, and E. Reimnitz, editors. The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press, Inc., Orlando, Florida.

Overeem, I., R. S. Anderson, C. W. Wobus, G. D. Clow, F. E. Urban, and N. Matell. 2011. Sea ice loss enhances wave action at the arctic coast. Geophysical Research Letters 38:1–6. doi: 10.1029/2011GL048681.

Perovick, D., S. Gerland, S. Hendricks, W. Meier, M. Nicolaus, and M. Tschudi. 2014. Sea Ice. Pages 32–38 *in* M. O. Jeffries, J. Richter-Menge, and J. E. Overland, editors. The Arctic Report Card: 2014. Retrieved from http://www.arctic.noaa.gov/reportcard.

Piersma, T. 1987. Hop, skip or jump. Constraints on migration of arctic waders by feeding, fattening, and flight speed. Limosa 60:185–194.

Piersma, T. 2002. Energetic bottlenecks and other design constraints in avian annual cycles. Integrative and Comparative Biology 42:51–67.

Piersma, T., J. A. van Gils, P. De Goeij, and J. van der Meer. 1995. Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. Journal of Animal Ecology 64:493–504.

Pisaric, M. F. J., J. R. Thienpont, S. V Kokelj, H. Nesbitt, T. C. Lantz, S. Solomon, and J. P. Smol. 2011. Impacts of a recent storm surge on an arctic delta ecosystem examined in the context of the last millennium. Proceedings of the National Academy of Sciences of the United States of America 108:8960–8965. doi: 10.1073/pnas.1018527108.

Ramenofsky, M. 1990. Fat storage and fat metabolism in relation to migration. Pages 214–231 *in* E. Gwinner, editor. Bird Migration: Physiology and Ecophysiology. Springer-Verlag, New York.

Rampal, P., J. Weiss, C. Dubois, and J. M. Campin. 2011. IPCC climate models do not capture Arctic sea ice drift acceleration: consequences in terms of projected sea ice thinning and decline. Journal of Geophysical Research: Oceans 116:1–17. doi: 10.1029/2011JC007110.

Reimnitz, E. R. K., and D. K. Maurer. 1979. Effects of storm surges on the Beaufort Sea coast, northern Alaska. Arctic 32:329–344.

Ribeiro, P. J., and P. J. Diggle. 2013. Package geoR. http://www.leg.ufpr.br/geoR.

Skagen, S. K. 2006. Migration stopovers and the conservation of arctic-breeding Calidridine sandpipers. Auk 123:313–322.

Steimle, F. W., and R. J. Terranova. 1985. Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. Journal of Northwest Atlantic Fisheries Science 6:117–124.

Taylor, A. R., R. B. Lanctot, A. N. Powell, S. J. Kendall, and D. A. Nigro. 2011. Residence time and movements of postbreeding shorebirds on the northern coast of Alaska. Condor 113:779–794. doi: 10.1525/cond.2011.100083.

Taylor, A. R., A. N. Powell, D. A. Nigro, and S. J. Kendall. 2010. Distribution and community characteristics of staging shorebirds on the northern coast of Alaska. Arctic 63:451–467.

USGS. 2012. Water-resources data for the United States, 2012: U.S.G.S. water-data report WDR-US-2012, site 15955000. wdr.water.usgs.gov/wy2012/pdfs/15955000.2012.pdf.

Van Gils, J. a., S. R. De Rooij, J. Van Belle, J. Van Der Meer, A. Dekinga, T. Piersma, and R. Drent. 2004. Digestive bottleneck affects foraging decisions in Red Knots *Calidris canutus*. I. Prey choice. Journal of Animal Ecology 74:105–119. doi: 10.1111/j.1365-2656.2004.00903.x.

Van de Kam, J., B. Ens, T. Piersma, and L. Zwarts. 2004. Food. Pages 147–227 *in* Shorebirds: An Illustrated Behavioural Ecology. KNNV Publishers, Utrecht.

Van de Pol, M., B. J. Ens, D. Heg, L. Brouwer, J. Krol, M. Maier, K. M. Exo, K. Oosterbeek, T. Lok, C. M. Eising, and K. Koffijberg. 2010. Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? Journal of Applied Ecology 47:720–730. doi: 10.1111/j.1365-2664.2010.01842.x.

Vermaire, J. C., M. F. J. Pisaric, J. R. Thienpont, C. J. Courtney Mustaphi, S. V. Kokelj, and J. P. Smol. 2013. Arctic climate warming and sea ice declines lead to increased storm surge activity. Geophysical Research Letters 40:1386–1390. doi: 10.1002/grl.50191.

Wacasey, J. W., and E. G. Atkinson. 1976. Energy values of marine benthic invertebrates from the Canadian Arctic. Marine Ecology Progress Series 39:243–250.

Walsh, J. E. 2008. Climate of the Arctic marine environment. Ecological Applications 18:S3–S22.

Warnock, N. 2010. Stopping vs. staging: the difference between a hop and a jump. Journal of Avian Biology 41:621–626. doi: 10.1111/j.1600-048X.2010.05155.x.

Wissing, T. E., and A. D. Hasler. 1971. Intraseasonal change in caloric content of some freshwater invertebrates. Ecology 52:371–373.

Yates, M. G., J. D. Goss-Custard, S. McGrorty, K. H. Lakhani, S. dit Durell, R. T. Clarke, W. E. Rispin, I. Moy, T. Yates, R. A. Plant, and A. J. Frost. 1993. Sediment characteristics, invertebrate densisites and shorebird densisites on the inner banks of the Wash. Journal of Applied Ecology 30:599–614.

Table 4.1. The caloric totals of the most common invertebrate taxa for three Beaufort Sea river deltas during early (21 July – 1 August), mid (1 – 8 August), and late (10 – 22 August) sample sessions.

	Canning		Okpilak/Hulahula			Jago		
		Late	Early	Mid	Late	Early	Mid	Late
2010								
Amphipoda		93,268	10,730	**	**	6,873	5,908	20,780
Chironomidae		**	65,692	26,689	70,444	54,308	25,052	97,813
Oligochaeta		73,546	26,522	22,477	29,182	49,935	8,888	61,968
2011								
Amphipoda	**	151,426	106	9,380	48,041	300	1,109	19,227
Chironomidae	**	**	34,038	89,898	115,409	25,573	89,060	72,240
Oligochaeta	231,551	298,834	206,292	488,689	1,177,222	107,710	146,198	146,424
Spionidae	9,522	76,176	**	**	42,849	**	**	**

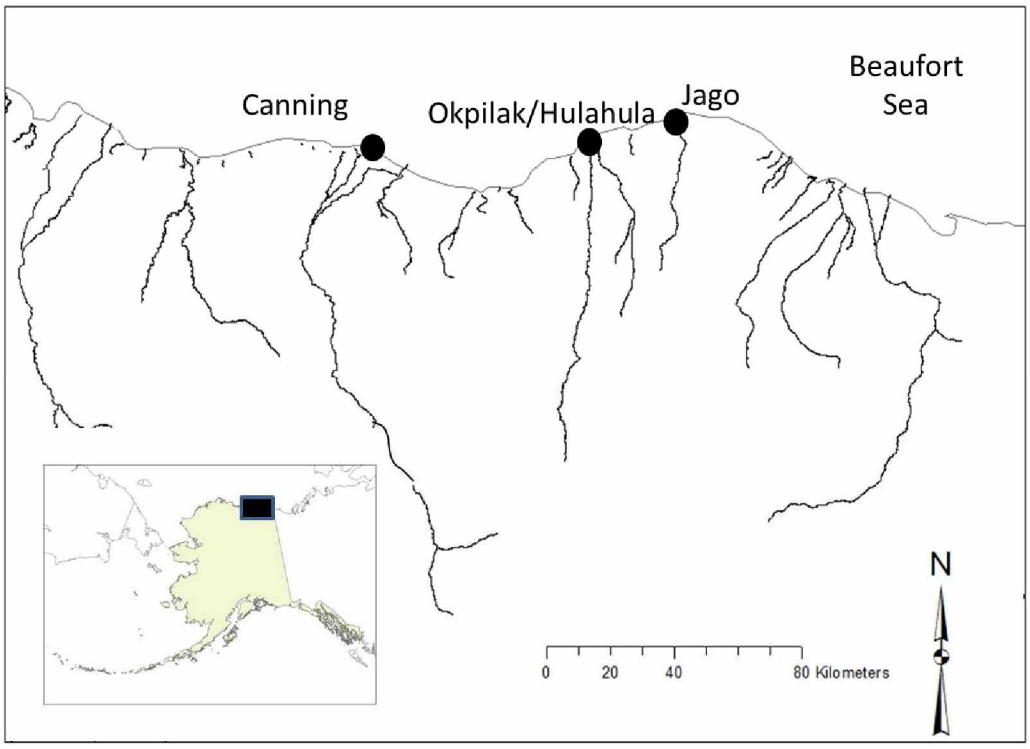

Figure 4.1. Location of three river deltas along the Beaufort Sea sampled for shorebird use (2009 – 2011) and invertebrate abundances and density (2010 – 2011).

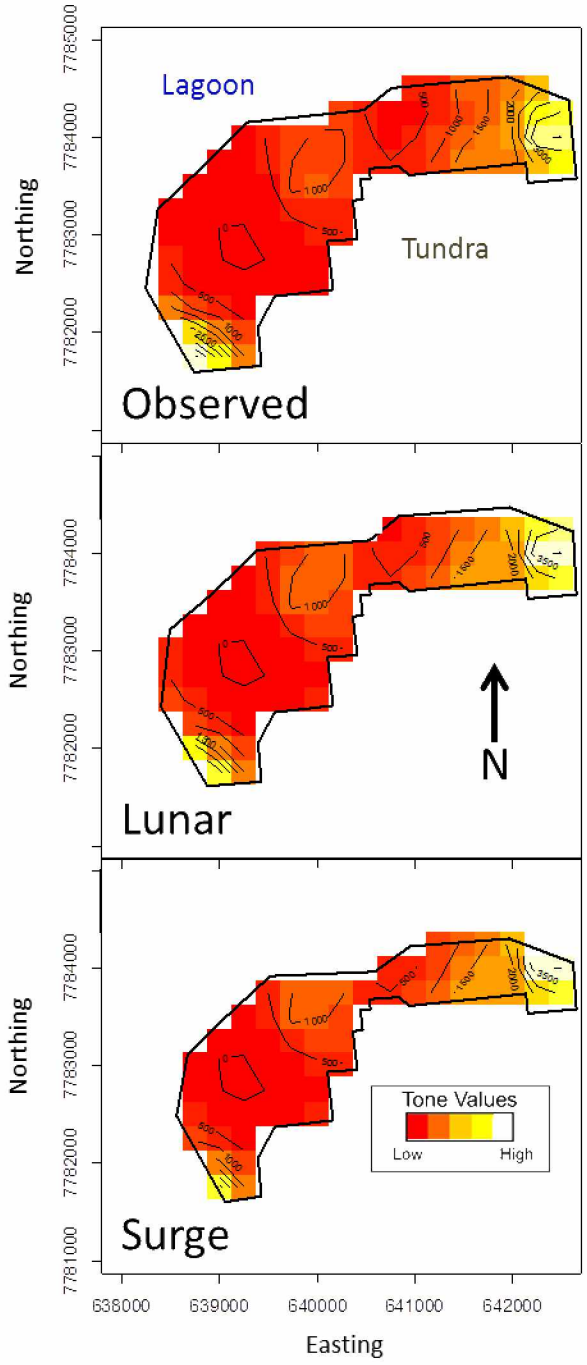

Figure 4.2. An example of the kriging layers for the Jago River delta during the late (10 – 22 August) sampling session, 2011. Layers reflect the changes in water levels depicted from observed water levels and models of lunar tides and an average storm surge.

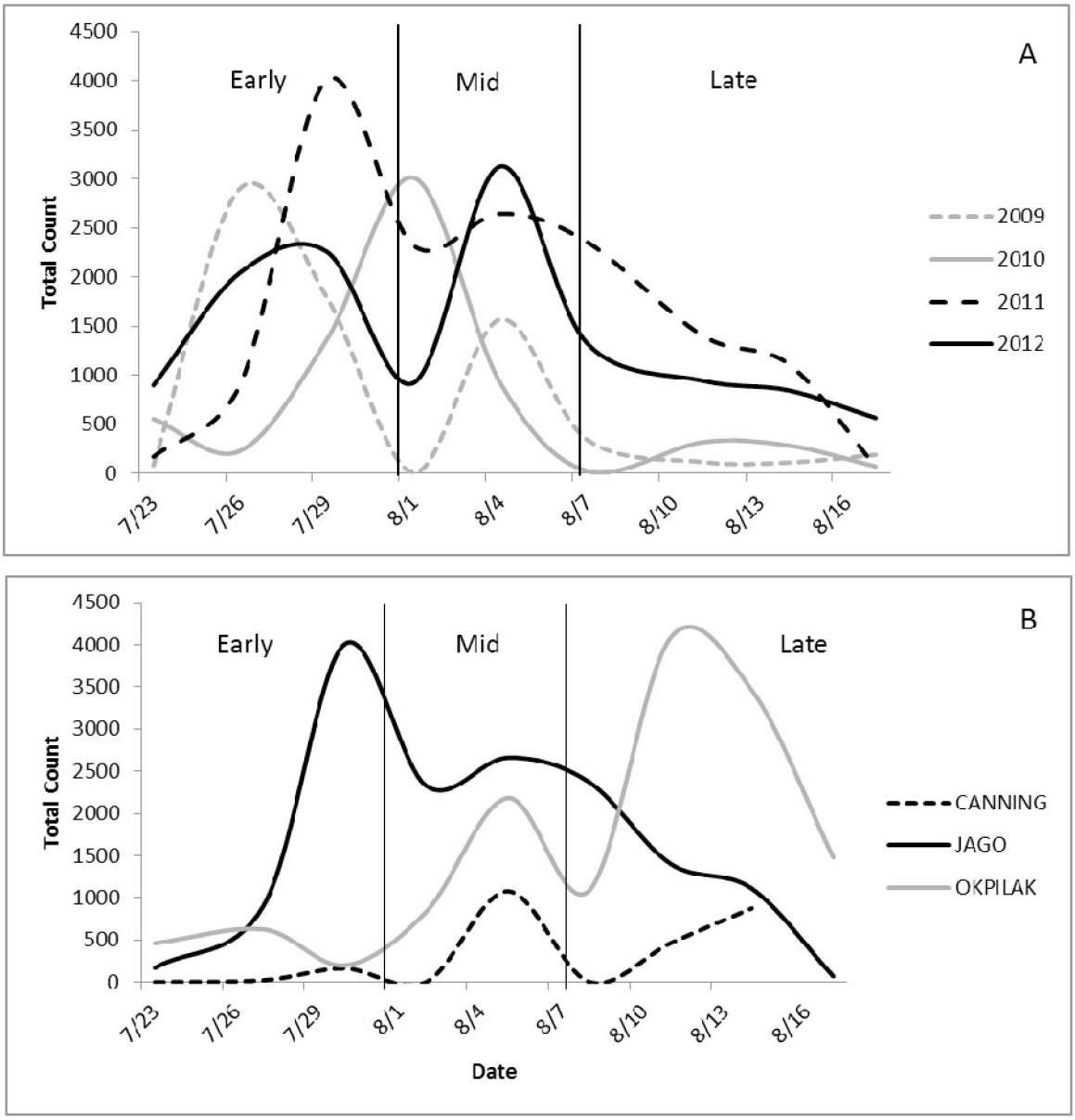

Figure 4.3. Phenology of fall migration for hatch-year Semipalmated Sandpipers at river deltas along the Beaufort Sea coast. A) Counts at the Jago River Delta 2009 – 2012. B) Counts at three deltas, 2011. Numbers are raw counts of Semipalmated Sandpipers during each survey day.

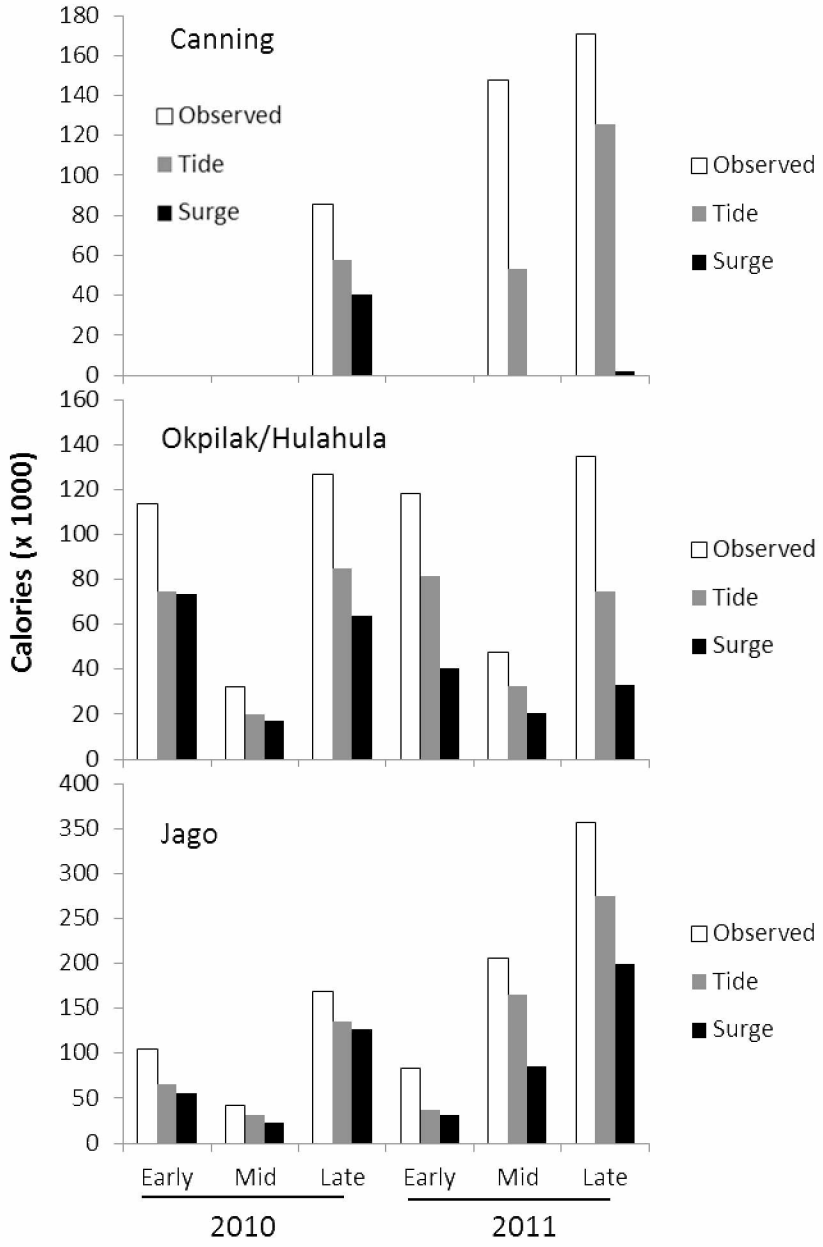

Figure 4.4. Changes in calories derived from invertebrate prey among three Beaufort Sea river deltas under three scenarios: observed water levels, modeled lunar tides, and modeled surge events, 2010 – 2011. The only model that completely inundated the delta occurred at the Canning delta during a mid (1 – 8 August) session as the result of a storm surge event.

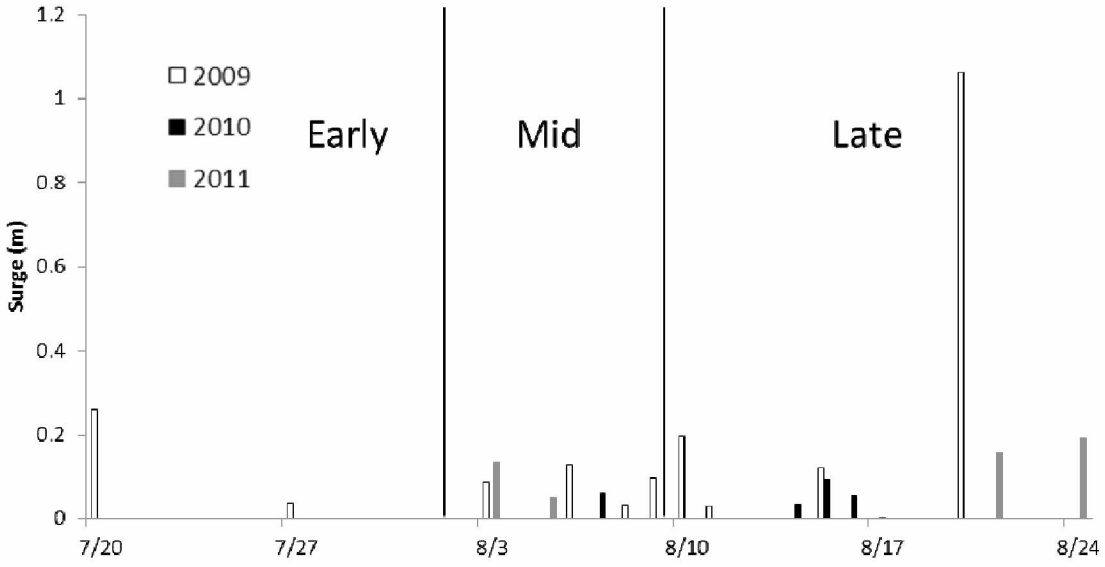

Figure 4.5. Date and heights of actual storm surge events along the Beaufort Sea coast during fall migration of Semipalmated Sandpipers, 2009 – 2011. Surge events were observed at all three river deltas (Canning, Okpilak/Hulahula, and Jago).

5 Conclusions

I investigated three aspects of stopover ecology of Semipalmated Sandpipers foraging at coastal deltas on the Beaufort Sea coast, Alaska (Figure 5.1). First, I characterized the benthic macroinvertebrate communities living within the mudflats within three river deltas. I also quantified the distribution and abundance of invertebrates, and explored the trophic distribution of these invertebrates within the mudflat community. Stable isotope analysis allowed me to describe the origin of carbon consumed by invertebrates in intertidal habitats. My second research question focused on the foraging ecology of Semipalmated Sandpipers feeding on benthic invertebrates at the river deltas. I report the distribution of birds and how it related to invertebrate distribution and abundance. I quantified fattening rates of shorebirds by measuring triglycerides in the blood of shorebirds I captured, and related this to habitat quality. Next, I described shorebird dependence on marine invertebrates using the stable isotope signature of invertebrates and shorebird plasma. Finally, I modeled changes in water levels due to lunar tides and storm surge events and how they impacted the availability of foraging habitat. I described the phenology of Semipalmated Sandpiper migration and how this related to the availability of forage based on abundance, distribution, and accessibility of macroinvertebrates.

5.1 Macroinvertebrate Ecology

Beaufort Sea intertidal habitat is locked in ice for nine months of the year, and I found that annual disturbance impacted the benthic invertebrate communities. Freshwater invertebrates have evolved to withstand freezing, and they overwinter in the frozen intertidal sediment. Marine invertebrates were not able to withstand freezing, and they recolonized intertidal habitats each summer from the deeper water of the lagoons. Some marine invertebrates that are common in more southern intertidal habitat were absent from Beaufort Sea intertidal areas because of the

movement from lagoons that was required. These included bivalves and many polychaete worms common at more southern deltas.

The water on the deltas was fresh water for the most part, with zero salinity, except for small patches with higher salinity on the ends of the deltas. This explained the abundance of freshwater invertebrates that I observed, and why there were fewer freshwater invertebrates at the Canning River delta, which was slightly more saline due to its proximity to the lagoon inlet and marine water. The persistence of delta freshwater communities may be in jeopardy in the future if expected increases in sea level are realized (Proshutinsky and Bourke 2001, Ritchter-Menge et al. 2008), if there is a significant storm surge event (Pisaric et al. 2011, Vermaire et al. 2013), or if summer river discharge declines when upstream glaciers melt (Nolan et al. 2011). Disappearance of the freshwater invertebrate community would have a drastic impact on the available forage for migrating shorebirds.

I hypothesized that freshwater invertebrates would consume different food than marine invertebrates based on their ecological origins, and that the isotopic signatures of the two ecological groups would reflect terrestrial and marine carbon sources; however, my results did not support my original predictions. Instead, I found that freshwater and saltwater invertebrates had similar isotopic signatures indicating that they were foraging on items originating from the same carbon source, which was a mixture of terrestrial- and marine-derived carbon. The only taxon with a different carbon source was Tipulidae, a freshwater invertebrate with a lower isotopic signature than the available carbon sources, which may be due to consumption of bacteria (Kirchman 1994, Fry 2006).

The distributions of macroinvertebrate taxa were patchy across deltas, although the invertebrate communities were similar among the deltas. The differences that I observed among

invertebrate communities can be explained by higher salinity at the Canning River delta that resulted in Chironomidae not being present and Spionidae being more common. Beyond investigating the distribution of invertebrates, I explored the habitat preferences of Chironomidae and Oligochaeta, and found a preference for delta habitats with higher moisture and finer grain size. Like other aspects of invertebrate ecology, the preference for fine sediments could be impacted by climate warming if melting glaciers disappear (Nolan et al. 2011) and fine sediment that originates from glaciers is replaced by coarser-grained sediment.

It is difficult to quantify the frequency of change in intertidal invertebrate communities on the Beaufort Sea coast because my research is one of the first comprehensive studies to describe them. However, negative impacts to invertebrate communities seem to be inevitable due to the increasing number of climate change threats predicted to impact the Beaufort Sea coast. Disturbance to the invertebrate community would directly impact migrating shorebirds that stop at these deltas during their fall migration and fish that feed on the invertebrates when water levels are higher. Furthermore, these impacts could influence higher trophic levels and the subsistence traditions of Native communities along the Beaufort Sea.

5.2 Semipalmated Sandpiper Feeding Ecology

I found tens of thousands of Semipalmated Sandpipers using river deltas as stopover sites after nesting on the Arctic coastal plain. Beaufort Sea deltas are the first "hop" for many of these fall migrants (Taylor et al. 2011), and I found about 98% of my detections were hatch-year birds, suggesting that adult birds are starting their migration using another route. River delta habitats seem to provide a vital resource to first-year birds as they begin their migration based on the large numbers of young birds foraging here. Many of the hatch-year birds that I captured were still growing based on short wing-chord measurements and feather tracts that were not fully

grown. Young birds starting their migration and finishing development probably need extra resources, and may find these extra resources at coastal river deltas.

When I compared migration among deltas (Table 5.1), there were more birds using the Jago Delta than the other two deltas, and the peak in migration was approximately 10 – 12 days earlier at the Jago Delta compared to the other two deltas. Interestingly, the Jago Delta is farthest east, while the birds are migrating from west to east. Migrating shorebirds must pass over the other two deltas before deciding to stopover at the Jago Delta. I might have suggested that forage was better at the Jago than the other two deltas; however, in comparing triglyceride levels in shorebird blood among deltas, I found no differences, which indicates there was no difference in habitat quality among deltas. According to triglyceride levels, birds using any of the deltas were able to acquire the resources needed. This also suggests that birds selected areas during periods when foraging there was profitable, and I found more shorebirds in areas with higher invertebrate abundance, which helps support the idea that shorebirds are selecting areas that favor energy transfer. Considering these results, it seems like the higher numbers are a response to better access to forage at the Jago Delta early in migration than at the other two deltas.

I also explored shorebird dependence on delta habitat by comparing the isotopic signature of blood serum samples from Semipalmated Sandpipers with invertebrate signatures from deltas and upland tundra. There was a distinct separation between the isotopic signatures of delta and upland tundra invertebrates. In the beginning the shorebirds reflected a mixed signature from deltas and upland areas, but later in the migration the shorebird isotopic signature reflected delta habitats only. It is likely that shorebirds were feeding on marine invertebrates earlier as well, but that the upland signature was still present in their tissues. The marine signature in the serum

indicates a dependence on delta invertebrates, but future research should try investigating why shorebirds need these marine resources. Semipalmated Sandpipers stopping at the Bay of Fundy are thought to select for amphipods because they are high in Omega-3 fatty acids that are supposed to improve flight efficiency (Maillet and Weber 2006), and it would be helpful to find out if shorebirds stopping at Beaufort Sea deltas were foraging there for similar reasons.

Finally, I explored the diet of Semipalmated Sandpipers using Bayesian mixing models that incorporated isotopic values for birds and delta invertebrates. The birds' diet was different among the three deltas, suggesting diet changed depending on invertebrate availability. Some selection of certain taxa may also occur since I found that the taxon in the highest proportion in the diet was not always the taxon in highest abundance on the delta. Proportions of invertebrate taxa in the diet are not always accurate in these analyses, however. One credible result was there was no evidence of Semipalmated Sandpipers feeding on Tipulidae larvae, which were common at all of the deltas and expected to be common forage taxa. This could be a demonstration of species partitioning invertebrate prey among different shorebird species, because Tupilidae larvae could be a forage food more commonly consumed by Dunlin (*Calidris alpina*), which are documented to feed on this taxa.

5.3 Water Levels

The water level on delta mudflats along the Beaufort Sea is just as important for shorebird access to foraging areas as other factors such as invertebrate abundance and distribution. The diurnal lunar tide along the Beaufort Sea coast is relatively low with a maximum tide of 30 cm compared to more temperate areas, and at most "high" tides there is still foraging habitat available for shorebirds. I found the greatest access to foraging habitat occurred late in the migration season, but the peak in shorebird migration was early in migration.

Furthermore, climate change has the potential to allow birds to migrate even earlier, which will further increase the temporal distance between the peak in migration and the peak in forage availability. As further support, I observed lower triglyceride levels early in the season suggesting that fewer food resources during this time of the migration may leave shorebirds less prepared for their southern migration.

Storm surges are also common but random events on the Beaufort Sea coast. These wind driven storm events can have a dramatic impact on water levels and in some cases can completely inundate a mudflat for multiple days. Storm surges occurred more after 1 August, but they are expected to occur earlier and more frequently as storm frequency increases and sea ice melts due to climate change (Overeem et al. 2011). Sea ice has a dampening effect on wave action that leads to storm surge. Furthermore, sea level rise will increase the impact of storm surge events on intertidal habitat and shorebird access to foraging areas (Craik et al. 2015). Past storm surges have even impacted meiofauna communities with lasting effects (Pisaric et al. 2011, Vermaire et al. 2013), and a change in meiofauna on delta mudflats could impact higher trophic levels including benthic macroinvertebrates that are important shorebird forage.

In summary my research helps quantify the importance of Beaufort Sea deltas to migrating shorebirds, especially juvenile Semipalmated Sandpipers. However, it is still difficult to describe how important these sites are to fall migration in terms of their effect on the success of fall migration for juvenile sandpipers. Despite the fact that I found considerable differences among the three deltas (Table 5.1), all of the deltas were used by significant numbers of migrating shorebirds and thus are important for the first "hops" of the fall migration of hatch-year Semipalmated Sandpipers that were produced on the coastal plain of northern Alaska. The Jago Delta was important for early migrants, while the Okpilak/Hulahula was used by large

flocks of migrants late in the season. I have learned a tremendous amount about the factors that drive macroinvertebrate abundance and distribution on coastal river deltas. These are critical resources for young shorebirds produced on the coastal plain of Alaska, and thus it can be assumed they play a role in successful fall migration and ultimately first-year survival. The loss of any one of these sites may jeopardize that success and survival. Hopefully future research can tackle these questions.

5.4 References

Craik, S. R., A. R. Hanson, R. D. Titman, and L. Matthew. 2015. Potential impacts of storm surges and sea-level rise on nesting habitat of Red-breasted Mergansers (*Mergus serrator*) on barrier islands in New Brunswick, Canada. Waterbirds 38:77–85.

Fry, B. 2006. Stable Isotope Ecology. Springer Verlag, New York.

Kirchman, D. L. 1994. The uptake of inorganic nutrients by heterotrophic bacteria. Microbial Ecology 28:255–271. doi: 10.1007/BF00166816.

Maillet, D., and J. M. Weber. 2006. Performance-enhancing role of dietary fatty acids in a long-distance migrant shorebird: the Semipalmated Sandpiper. Journal of Experimental Biology 209:2686–95. doi: 10.1242/jeb.02299.

Nolan, M., R. Churchwell, J. Adams, J. McClelland, K. D. Tape, S. Kendall, A. Powell, K. Dunton, D. Payer, and P. Martin. 2011. Predicting the impact of glacier loss on fish, birds, floodplains, and estuaries in the Arctic National Wildlife Refuge. Pages 49–54 *in* C. N. Medley, G. Patterson, and M. J. Parker, editors. Observing, Studying, and Managing for Change. US Geological Survey Scientific Investigations Report 2011- 5169, Reston, Virginia.

Overeem, I., R. S. Anderson, C. W. Wobus, G. D. Clow, F. E. Urban, and N. Matell. 2011. Sea ice loss enhances wave action at the Arctic coast. Geophysical Research Letters 38:1–6. doi: 10.1029/2011GL048681.

Pisaric, M. F. J., J. R. Thienpont, S. V Kokelj, H. Nesbitt, T. C. Lantz, S. Solomon, and J. P. Smol. 2011. Impacts of a recent storm surge on an arctic delta ecosystem examined in the context of the last millennium. Proceedings of the National Academy of Sciences of the United States of America 108:8960–8965. doi: 10.1073/pnas.1018527108.

Proshutinsky, A., and R. H. Bourke. 2001. Sea level rise in the Arctic Ocean. Geophysical Research Letters 28:2237–2240.

Ritchter-Menge, J., A. Proshutinsky, V. Romanovsky, D. Russell, C. D. Sawatzk, M. Simpkins, R. Armstrong, I. Ashik, L.-S. Bai, D. Bromwich, J. Cappelen, E. Carmack, J. Comiso, B. Ebbinge, I. Frolov, J. C. Gascard, M. Itoh, G. J. Jia, R. Krishfield, F. McLaughlin, W. Meier, N. Mikkelsen, J. Morison, T. Mote, S. Nghiem, D. Perovich, I. Polyakov, J. D. Reist, B. Rudels, U. Schauer, A. Shiklomanov, V. Sokolov, M. Steele, M.-L. Timmermans, J. Toole, B. Veenhuis, D. Walker, J. E. Walsh, M. Wang, A. Weidick, and C. Zöckler. 2008. Arctic Report Card 2008. Retrieved from http://www.arctic.noaa.gov/reportcard.

Taylor, A. R., R. B. Lanctot, A. N. Powell, S. J. Kendall, and D. A. Nigro. 2011. Residence time and movements of postbreeding shorebirds on the northern coast of Alaska. Condor 113:779–794. doi: 10.1525/cond.2011.100083.

Vermaire, J. C., M. F. J. Pisaric, J. R. Thienpont, C. J. Courtney Mustaphi, S. V. Kokelj, and J. P. Smol. 2013. Arctic climate warming and sea ice declines lead to increased storm surge activity. Geophysical Research Letters 40:1386–1390. doi: 10.1002/grl.50191.

Table 5.1. Comparison of the three river deltas where Semipalmated Sandpipers stopped during fall migration (2010 – 2012) on the Beaufort Sea coast, AK.

Relative Characteristics	Canning	Okpilak/Hulahula	Jago
Size (ha)	290	740	650
Location	west	central	east
Glacially fed	no	yes	yes
Sediment type	sandier	siltier	siltier
Salinity	partially saline	freshwater	freshwater
Invertebrate Abundance (peak)[1]	1,075	1,648	1,241
Peak Invertebrates (time)	late	late	late
Dominant Invertebrate Taxa	Oligochaeta	Oligochaeta	Oligochaeta/Chironomidae
Estimated Calories (average)	134,791	95,523	160,376
Peak Shorebirds (time)	mid/late	late	early
Shorebird Abundance (peak)	1,000	4,000	4,000
Shorebird Diet	Spionidae	Chironomidae	Amphipoda
Storm Surge Impact	highest	medium	lowest
Avian Predator Cover	low	high	low

[1] The discrepancy between invertebrate abundance and estimated calories is due to abundance being calculated as a total and calories an average.

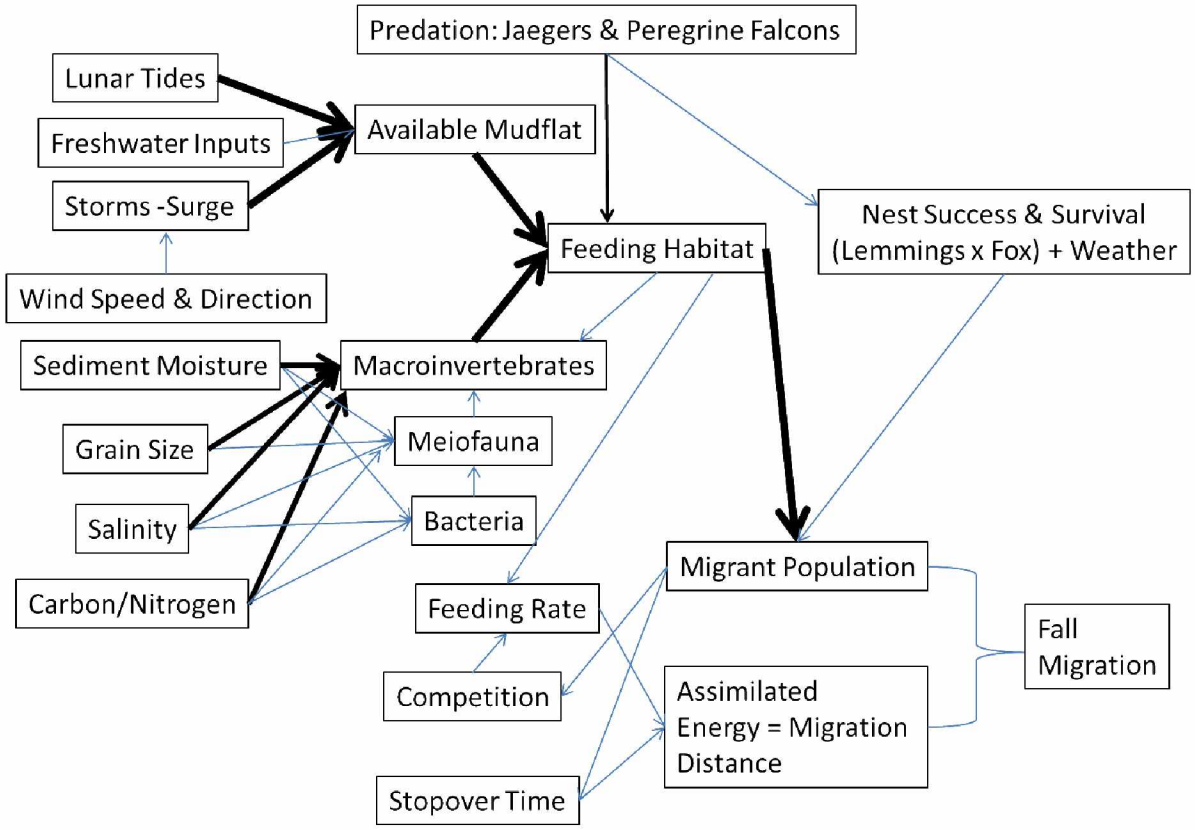

Figure 5.1. Conceptual model describing shorebird stopover ecology at delta mudflats on the coast of the Beaufort Sea, AK. The darkened arrows depict pathways described in this research, and the width of the arrow displays my perception of the pathway's importance.

Appendix A:

Letters of Consent from Authors

Stephen Brown

10/19/15

To: Roy Churchwell

Hi Roy,

This email is to provide permission to use our manuscript in your dissertation.

Congratulations on your successful defense!

All my best,

Stephen

Steve Kendall

10/19/15

To: Roy Churchwell, Stephen Brown, Abby Powell

Hi Roy,

You have my permission to use our manuscripts in your dissertation. Please let me know if this email is sufficient authorization or if you need something else.

Thanks,

Steve

Appendix B:

Supplemental Data

Table B.1. Stable isotope values for red blood cells and plasma from Semipalmated Sandpipers on the Beaufort Sea coast, AK 2010 – 2011.

	Blood				Plasma					
Sample Name	**Conc N (%)**	**Conc C (%)**	**$\delta^{15}N$ (‰)**	**$\delta^{13}C$ (‰)**	**Conc N (%)**	**Conc C (%)**	**$\delta^{15}N$ (‰)**	**$\delta^{13}C$ (‰)**	**Session**	**Delta**
B002D	15.32	48.39	7.04	-25.46	9.10	46.84	7.92	-23.22	Early	Jago
B14100	16.15	50.61	6.25	-27.48	8.22	44.02	4.42	-24.50	Early	Okpilak
B56301	15.78	50.19	6.87	-26.46	9.43	47.46	7.86	-27.47	Early	Canning
B56305	11.33	36.44	7.83	-27.63	9.69	44.99	9.18	-25.96	Early	Canning
B56306	15.00	48.04	6.12	-27.10	9.04	44.30	7.13	-27.63	Early	Canning
B56307	13.86	44.57	6.28	-26.61	9.33	45.71	7.66	-28.84	Early	Canning
B56308	13.63	43.94	6.02	-26.94	9.35	45.91	7.60	-26.90	Early	Canning
B56313	15.90	50.47	6.42	-24.25	9.09	46.94	7.68	-26.20	Early	Canning
B56317	14.73	46.70	6.25	-25.57	9.02	45.50	8.87	-24.67	Early	Canning
B56324	14.06	44.50	6.88	-28.43	9.09	44.26	8.16	-27.92	Early	Canning
B56331	14.98	48.52	7.09	-25.68	8.74	47.17	7.93	-22.12	Late	Canning
B56334	14.39	46.56	6.04	-25.02	8.97	49.17	7.45	-22.86	Late	Canning
B56374	15.81	50.02	7.84	-27.57	9.38	46.05	8.61	-24.10	Early	Okpilak
B56377	14.92	47.32	6.97	-23.76	8.20	46.46	6.55	-20.26	Early	Okpilak
B56380	15.95	50.30	4.22	-25.33	8.69	48.02	5.32	-23.70	Early	Okpilak
B56381	16.01	49.30	6.88	-24.63	9.15	46.26	8.17	-25.09	Early	Okpilak
B56392	15.58	50.23	7.09	-25.84	9.34	43.35	8.08	-27.68	Early	Okpilak
B56393	14.88	47.45	8.23	-26.90	8.74	44.62	8.12	-25.01	Early	Jago
B56395	14.82	48.34	7.25	-25.80	8.78	45.09	8.27	-26.96	Early	Jago
B56396	15.08	48.16	6.20	-26.40	9.24	45.54	8.85	-26.08	Early	Jago
B56398	15.70	49.56	5.89	-23.55	8.78	47.10	7.55	-26.20	Early	Jago
B56411	11.51	36.83	7.99	-26.44	9.67	44.37	8.57	-27.49	Early	Jago
B56415	15.17	48.08	5.73	-27.24	12.26	60.44	6.47	-25.94	Early	Jago
B56418	15.32	49.07	5.75	-25.54	9.00	44.60	7.85	-25.85	Early	Jago
B56419	14.70	47.32	7.83	-27.80	8.33	42.34	7.76	-25.08	Early	Jago
B56421	13.41	42.97	7.31	-26.20	9.35	44.75	7.89	-23.23	Early	Jago
B56426	14.39	46.24	7.00	-25.34	8.46	45.97	7.39	-20.86	Late	Jago

Table B.1 Continued

B56431	14.95	47.96	8.01	-25.17	8.80	42.98
B56433	15.64	50.55	7.32	-24.87	8.80	44.84
B56435	14.45	46.19	6.76	-22.84	9.37	49.56
B56461	15.54	50.45	7.92	-27.42	8.68	44.2
B56462	14.30	47.54	5.74	-23.10	7.42	49.50
B56471	15.43	50.06	7.88	-27.07	9.06	46.00
B56475	15.51	50.03	7.59	-26.62	8.76	46.95
B56487	15.61	49.82	5.99	-24.35	6.26	32.34
B56488	15.28	48.90	7.48	-26.21	8.53	46.95
B56490	16.13	50.61	5.73	-24.77	5.88	29.98
B56493	15.64	50.25	6.48	-25.85	7.60	37.21
B56494	15.63	50.37	6.65	-25.92	8.79	43.17
B56505	15.81	50.03	4.45	-25.94	8.72	42.05
B56519	15.24	49.54	4.84	-26.60	8.73	41.86
B56520	14.83	47.42	5.14	-25.63	8.39	40.97
B56525	15.75	50.90	6.22	-24.32	8.39	48.13
B56526	15.39	49.74	6.96	-25.40	7.89	47.14
B56550	14.13	48.11	3.84	-24.81	8.49	41.16
B56556	15.43	49.00	6.94	-26.45	9.28	44.21
B86110	15.73	50.00	7.07	-24.12	8.35	46.98
B86111	15.20	48.12	7.06	-24.54	8.96	42.14
B86112	14.79	47.22	5.88	-23.49	8.93	46.01
B86113	15.92	50.68	6.65	-22.23	7.30	46.61
B86115	15.24	48.46	6.44	-24.94	9.02	45.68
B86120	15.30	51.07	7.32	-24.46	8.45	47.63
B86125	15.13	50.72	6.38	-24.89	8.97	48.69
B86126	14.89	49.53	6.94	-24.31	9.74	47.71
B86135	15.53	51.18	6.87	-24.74	8.88	47.73
B86137	15.77	51.12	5.22	-24.42	8.45	49.77

7.62	-21.30	Late	Jago
8.27	-24.24	Late	Jago
6.32	-19.94	Late	Jago
7.97	-25.45	Early	Canning
6.58	-25.77	Early	Canning
9.08	-24.45	Early	Canning
8.82	-25.28	Early	Canning
6.91	-20.15	Late	Okpilak
7.37	-19.88	Late	Okpilak
7.39	-19.74	Late	Okpilak
7.52	-21.77	Late	Okpilak
7.90	-21.53	Late	Okpilak
5.21	-25.13	Early	Okpilak
5.02	-25.20	Early	Okpilak
5.90	-22.28	Early	Okpilak
7.85	-22.11	Early	Okpilak
8.54	-24.35	Early	Okpilak
5.24	-24.10	Early	Okpilak
7.19	-25.92	Early	Okpilak
10.59	-21.22	Late	Jago
8.30	-20.50	Late	Jago
9.16	-21.47	Late	Jago
9.56	-21.44	Late	Jago
10.00	-22.60	Late	Jago
9.34	-22.53	Late	Canning
8.82	-21.53	Late	Canning
9.24	-21.66	Late	Canning
8.55	-22.34	Late	Canning
8.73	-23.59	Late	Canning

Table B.2. Shorebird species observed during shorebird surveys on delta study sites along the coast of the Arctic National Wildlife Refuge, AK, 2010 and 2011. Percent Days Observed is the percentage of days out of the total number of survey days for that year: Percent Juveniles is the percent juveniles of the total number of birds counted (excluding observations of birds of unknown age). Abundance is a relative abundance index of the total abundance for each species divided by three, the number of study sites.

		2010			2011		
Species	Scientific Name	% Days Obs.	% Juv.	Abund.	% Days Obs.	% Juv.	Abund.
Semipalmated Sandpiper	*Calidris pusilla*	95	98	3502	100	99	11013
Pectoral Sandpiper	*Calidris melanotos*	37	100	1608	90	99	795
Red-necked Phalarope	*Phalaropus lobatus*	53	6	484	100	15	1811
Dunlin	*Calidris alpina*	79	39	372	100	40	429
Stilt Sandpiper	*Calidris himantopus*	37	100	159	80	99	176
Black-bellied Plover	*Pluvialis squatarola*	74	5	150	90	0	289
Sanderling	*Calidris alba*	53	72	49	80	60	76
Baird's Sandpiper	*Calidris bairdii*	42	99	48	80	92	11
Western Sandpiper	*Calidris mauri*	47	97	34	80	97	262
American Golden Plover	*Pluvialis dominica*	37	81	20	60	30	11
White-rumped Sandpiper	*Calidris fuscicollis*	21	100	9	20	100	2
Red Phalarope	*Phalaropus fulicarius*	16	17	6	40	8	5
Ruddy turnstone	*Arenaria interpres*	37	87	6	60	75	11
Long-billed Dowitcher	*Limnodromus scolopaceus*	5	100	3	10	6	6
Bar-tailed Godwit	*Limosa lapponica*	11	100	1	10	100	1
Hudsonian Godwit	*Limosa haemastica*	**	**	**	10	100	1
Semipalmated Plover	*Charadrius semipalmatus*	11	50	1	30	0	1
Least Sandpiper	*Calidris minutilla*	**	**	**	10	100	1

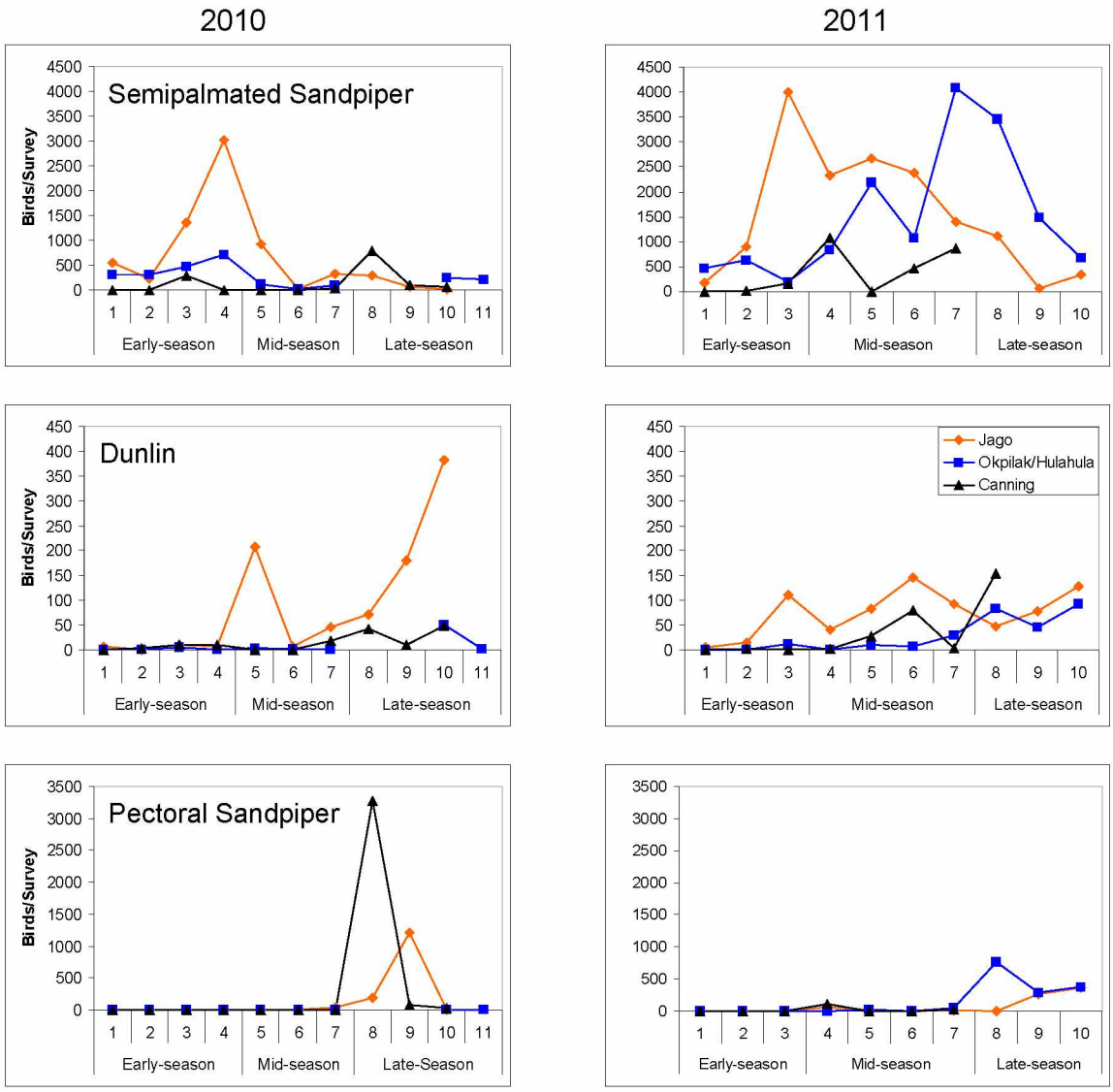

Figure B.1. Abundance of the three most abundant Calidrid shorebirds at the Canning, Okpilak/Hulahula, and Jago River Deltas, Arctic National Wildlife Refuge, 2010. The x-axis depicts surveys conducted every three days starting 20 July and ending 21 August in 2010 and starting 24 July and ending 20 August 2011. Surveys were not conducted to the end of the season at all sites, and surveys eight and nine were missed at the Okpilak/Hulahula in 2010.